CAUSES OF SHORT-TERM SEQUENTIAL CHANGES IN FOSSIL PLANT ASSEMBLAGES: SOME CONSIDERATIONS BASED ON A MIOCENE FLORA OF THE NORTHWEST UNITED STATES[1]

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ABSTRACT

Several geologic and edaphic factors as well as climate appear to exert control over types of fossil assemblages in successive stratigraphic sequences in the Miocene of eastern Oregon and western Idaho. Direct geological control of plant communities included volcanic activity (gaseous, pyroclastic, and liquid ejecta), which may have killed plants and disrupted communities by explosive force, noxious gases, and the burial or smothering effect of cinder and ash falls and mudflows (lahars). Indirect, longer-term effects are caused by tectonism in the immediate area (graben-horst shifts, regional uplift, basin development, etc.), and at a considerable distance (climatic modification, rain shadow, continentality). Fossil representation is also modified by transportability, distance of transport, and durability of plant matter; availability and permanence of favorable sites for preservation; the nature, rate, and continuity of sedimentation; and the extent of selective destruction of the vegetation. In the Succor Creek Formation, volcanism, tectonic activity, and fire have affected vegetation dynamics, resulting in the presence of successional communities that might otherwise be attributed to significant climatic change if stratigraphic control were lacking. Typically successional communities tend to develop toward stable forests unless or until disrupted by further disturbance. Intervals of non-deposition and/or erosion leave gaps of varying and unknown magnitudes in the stratigraphic sequences. The time represented by each of the several stratigraphic units is only a fraction of the total Succor Creek time (1–2 m.y.), probably a thousand to a few thousand years.

INTRODUCTION

The Succor Creek Flora is contained in a thick sequence of volcanic rocks along Succor Creek and the eastern part of the Owhyee River watershed in Malheur County of southeastern Oregon and Owyhee County of southwestern Idaho (Fig. 1). The area of the principal exposures is bounded on the west by the Owyhee River, on the east by the western end of the Snake River Plain, and exposures extend into and around the north end of the Owhyee Mountains on the south.

GEOLOGY

The rocks in the Owyhee area are a complexly interrelated series of basalt and rhyolite flows, rhyolitic ash-flow tuffs, air-fall volcaniclastics of ash and pumice, water-laid ash and lacustrine sediments ranging from a mixture of volcani-

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[1] We acknowledge with our sincere thanks: Dr. Alan Graham, Dr. Arthur R. Green, Dr. Lawrence E. Kittleman, Dr. Charles L. Rosenfeld, and Dr. Helen V. Smith for discussions and other assistance and information relative to the geology and the fossil plant collecting sites and collections of the Succor Creek area; Dr. J. Platt Bradbury for examination of diatom-rich samples; Curators of the Michigan State University Beal-Darlington Herbarium, Dr. John H. Beaman and Dr. Susan R. Kephart; and Loretta S. Satchell, Kurtis C. Kelley, and Catherine Caswell for field and laboratory assistance.

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ANN. MISSOURI BOT. GARD. 69: 676–734. 1982.
0026-6493/82/0676–0734/$05.95/0

clastic sediments to lignite and diatomite. Kittleman et al. (1965) summarized the surface geology and general stratigraphy and described several formations of Miocene and Pliocene age, including the Sucker Creek Formation.[3] The Sucker Creek Formation consists of "altered tuffs and volcanic sandstones, vitric tuffs, arkose sandstone, granite-cobble conglomerates, and carbonaceous volcanic shales" (Kittleman et al., 1965, p. 6).

The Type section (Fig. 1, locality 4) is about 200 m thick and contains only volcaniclastic rock, lignitic shales, and diatomite. Exposures at the northern end of the area measure more than 600 m in thickness (Fig. 1, loc. 15). Warner (1977), on the basis of four deep test holes drilled north and northeast of the area shown on Fig. 1, in the western end of the Snake River Plain (Fig. 2), has postulated the thickness in this deep part of the basin at about 2,000 m, the wells having penetrated nearly 1,500 m of strata identified as Sucker Creek Formation.

Near locality 15, a tabular basaltic flow, the "Bishop's Ranch Basalt," is included in the formation. A rhyolitic ash-flow tuff (Leslie Gulch Ash-Flow Tuff Member), which is lenticular in nature and about 300 m thick, is included in the Sucker Creek Formation about 20 km west of the Type section (loc. 4, Fig. 1). Lignites and lignitic shales from 1–10 m thick, are found in several local areas including the Coal Mine Basin (loc. 12), Whiskey Creek (loc. 3), McBride Creek (our "Shortcut" section, loc. 2), Rockville (loc. 1), Type locality and Rocky Ford section (loc. 4, 4a), and the Devils Gate section (loc. 9). Some of the sedimentary rocks have a vitric component that is usually altered to a greater or lesser extent, usually to montmorillonite minerals. Either glass shards or pseudomorphs of glass, altered to zeolitic minerals such as clinoptilolite and heulandite, are found in many of the fluvial and lacustrine beds. Some arkosic rocks contain a more complex suite of minerals, including sanidine and andesine, with quartz, biotite, and muscovite; and Kittleman et al. (1965) suggest that these may have been derived by water transport from granitic rocks of the Idaho Batholith (Fig. 2). Our own paleotopographic reconstructions suggest that this is unlikely in our study area and it is possible that the granitic core of the Owyhee's may have served as a more local source area.

The Sucker Creek Formation lies unconformably on a thick sequence of late Oligocene–early Miocene volcanics that were greatly faulted, uplifted, and eroded prior to the onset of a mid-Miocene episode of volcanism about 15 to 16 m.y.b.p. The Columbia River Group of mid-Miocene basalts (Fig. 3) is in part equivalent in age to the Sucker Creek Formation. The Sucker Creek is overlain unconformably by various late Miocene volcanics, including the Idavada Volcanics of early Pliocene age (Malde & Powers, 1962) and interfingers at the margins with the Columbia River Basalts. These Miocene rocks are considerably deformed by north-trending folds and northwest-trending faults (Fig. 3 and McBirney, 1978), which developed during the later Miocene, Pliocene, and Pleistocene.

The age of the Sucker Creek Formation has not been clearly established. A

[3] The original name "Succor" is now generally used but the spelling "Sucker" has been more extensively used. Kittleman used "Sucker Creek" when describing the Formation, which therefore has priority. Sucker will be used here in reference to the stratigraphic sequence (and time) included in the Formation. However, we are following recommended use of "Succor Creek" to refer to geographic area, stream, and flora.

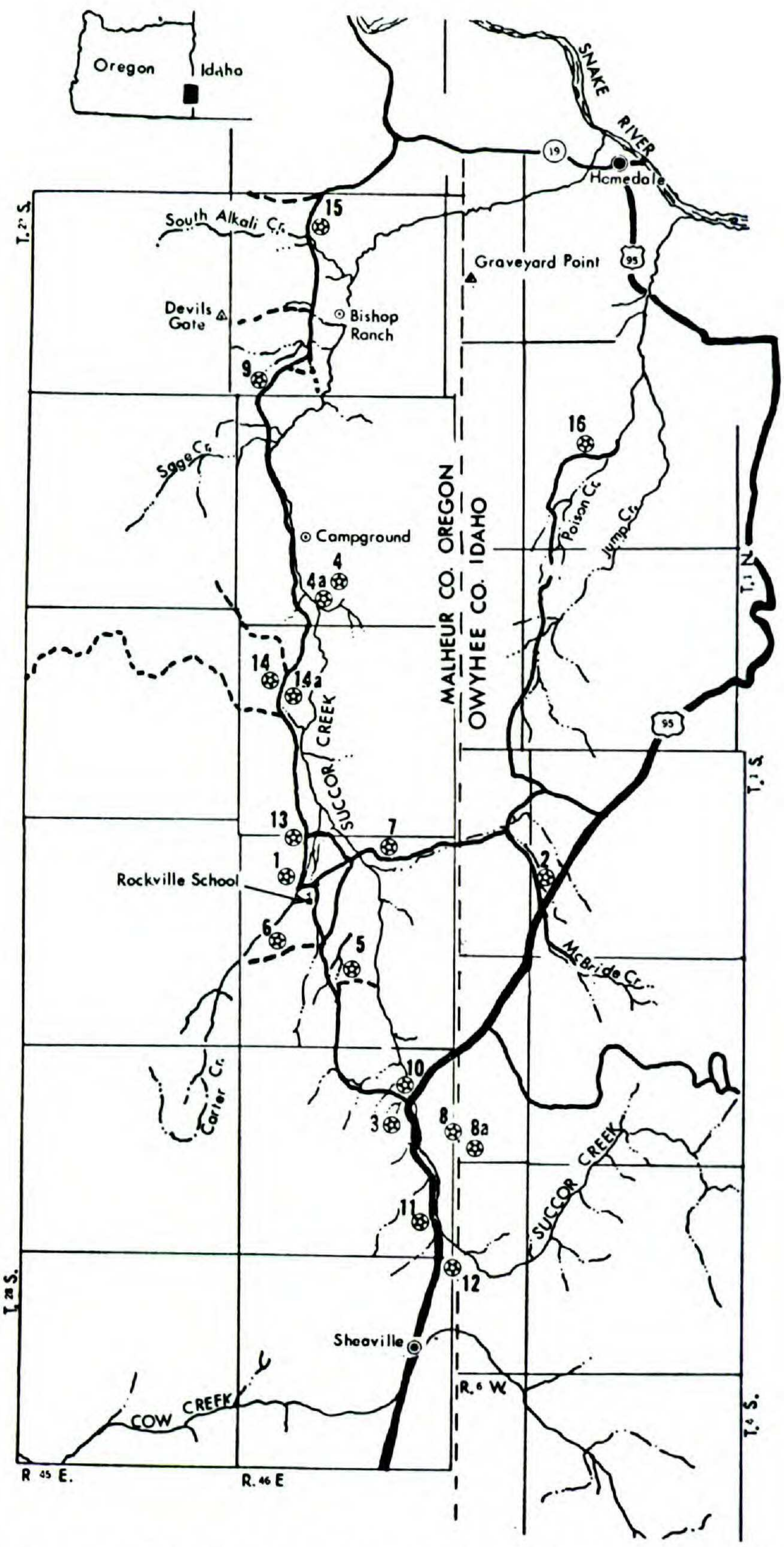


FIGURE 1. Index map of the Succor Creek area (Taggart & Cross, 1980*) showing the distribution of fossil plant localities and measured stratigraphic sections. Localities noted in this paper include the Whiskey Creek section (3), the Rockville section (1), the Shortcut section (2), the Rocky Ford (4a) and Type section (4), the Pine locality (7), and the Devils Gate section (9). * Reprinted with permission from Biostratigraphy of Fossil Plants, David L. Dilcher & Thomas N. Taylor, editors. Copyright 1980 by Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa.

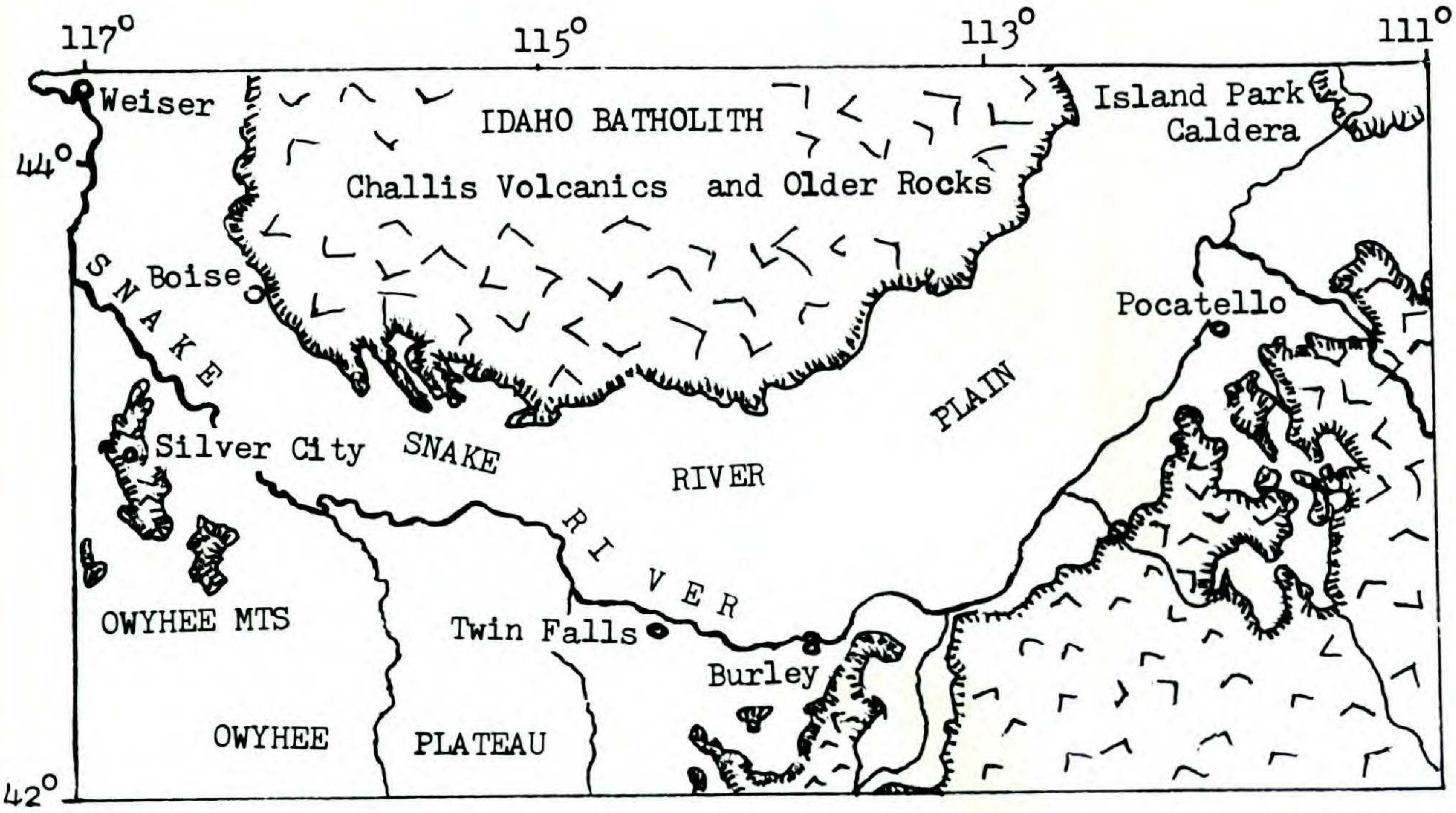


FIGURE 2. General physiographic map of southern Idaho and the Snake River Plain. The Succor Creek area lies along the Idaho-Oregon boundary between Silver City, in the Owyhee Mountains at the south, northward to about one-half the distance to the point where the Snake River intersects the Idaho-Oregon border. L-pattern area of pre-Miocene rock; hachures indicate the Owyhee Mountains and uplands bordering the Snake River Plain. (From Armstrong, Leeman & Malde, 1975, Amer. Jour. Sci. 275: 226, fig. 1.)

basalt sample taken from near our locality 3 (Fig. 1) was dated by Evernden and James (1964, p. 971, KA 1285) at 16.7×10^6 years, but neither the precise locality of the sample could later be verified by G. T. James, the collector, nor can the relationship of the basalt to the Succor Creek plant-bearing beds north of U.S. Highway 95 (near the Succor Creek bridge) be determined, because of extensive faulting in the area. This early Barstovian age agrees well with the age-determination based on mammal fossils by Scharf (1935) and Shotwell (*in* Kittleman et al., 1965, p. 7; see also Shotwell, 1968), from near the Type locality (loc. 4, possibly Unit 14, Fig. 10). Chaney and Axelrod (1959, p. 113) assigned a middle to late Miocene age to these plant-bearing beds on the basis of collections, probably taken near our locality 3 (Fig. 1). Kittleman obtained a 15.4 ± 0.9 m.y. age on sanidine and an 18.5 ± 1.7 m.y. age on glass shards from his Unit K-20 (our Unit 31) of the Type section (loc. 4, Fig. 10). Watkins and Baksi (1974) determined Normal polarity of the paleomagnetism in Owyhee Basalt, which overlies the Sucker Creek Formation in some parts of this area, with supporting age dates of 13.1–13.9 m.y.

SUCCOR CREEK FLORA

Knowlton (1898) described the first plants that were collected in this area by W. Lindgren, apparently below the base of our locality 3 and near our locality 6 (Fig. 1). Subsequently the flora was studied by Berry (1932), Brooks (1935), Arnold (1936a, 1936b, 1937), Smith (1938, 1939, 1940), and Chaney and Axelrod

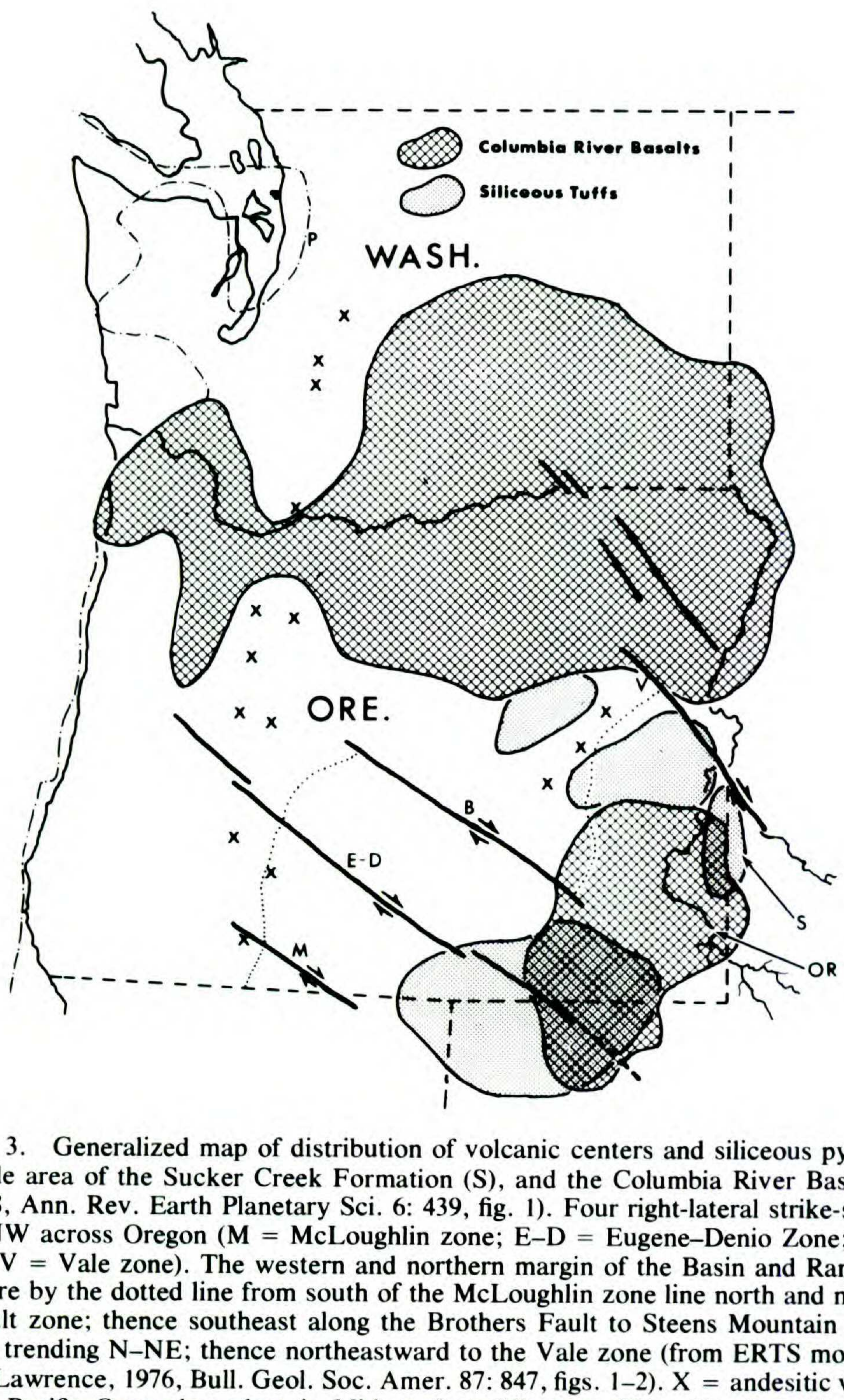


FIGURE 3. Generalized map of distribution of volcanic centers and siliceous pyroclastic tuffs, which include area of the Sucker Creek Formation (S), and the Columbia River Basalts (after McBirney, 1978, Ann. Rev. Earth Planetary Sci. 6: 439, fig. 1). Four right-lateral strike-slip fault zones extend W–NW across Oregon (M = McLoughlin zone; E–D = Eugene–Denio Zone; B = Brothers Fault zone; V = Vale zone). The western and northern margin of the Basin and Range Province is delimited here by the dotted line from south of the McLoughlin zone line north and northeast to the Brothers fault zone; thence southeast along the Brothers Fault to Steens Mountain Fault, a major normal fault trending N–NE; thence northeastward to the Vale zone (from ERTS mosaic of Oregon as shown in Lawrence, 1976, Bull. Geol. Soc. Amer. 87: 847, figs. 1–2). X = andesitic volcanic cones; ·—·—·— = Pacific Ocean boundary in Mid- to Late-Miocene; OR = Owyhee River; S = Succor Creek area. Arrows indicate the net direction of movement along faults and fault zones. The Snake River is, in part, occluded here by the line marking the Vale fault zone. The line of andesitic cones northward through Oregon and Washington marks the volcanoes of the present High Cascades.

(1959). Graham's extensive studies (1963, 1965) reported 69 species, representing 60 genera distributed among 47 families. He also conducted the first analysis of the spores and pollen in these strata. Taggart (1973) added seven new taxa to the flora.

The Succor Creek Flora is a composite of many florules based upon fossil plant specimens collected from at least 25 published localities. Historically, this has been considered to be one flora that accumulated intermittently for a period of one to two million years over a subdued, eroded, volcanic landscape, probably a plateau. Plant remains have been preserved in intermittently deposited, largely fluvially recycled, pyroclastics, i.e., ash, ash-flow tuffs, and weathering products of basalts and rhyolites, and in some direct ash-falls. Graham (1965) in his review of the fossils collected at 16 sites, stated (p. 16) ". . . There is no evidence of disproportionate representations suggesting significant variation in the age of the localities . . . it is likely that several basins were variously connected at different times . . . ," and, ". . . It must be assumed . . . that these basins were of approximately the same age, geologically, and that the Sucker Creek constitutes a single paleofloristic unit."

One exception to this concept of a "single flora" made up of many florules was introduced by Wolfe (1969, p. 88–89) where he states, ". . . The Succor Creek (late Miocene) and Rockville (middle Miocene) assemblages are here considered as distinct . . . ." Wolfe uses the age-date of 16.7 m.y., reported by Evernden and James (1964), to verify the age of the "Rockville" as middle Miocene, but has no age-date for the late Miocene, a situation that still exists. The latter age assignment was made (Wolfe, 1969, p. 89) on the basis that he interpreted the late Miocene assemblages to ". . . represent a cooler time interval than do the middle Miocene assemblages . . . ," and thus inferred that some of the Succor Creek florules were accumulated at a later time (late Miocene?) in a cooler climate, than the "Rockville." The identity of which of the florules he considered as "Rockville" is obscure. Though "Rockville" has been occasionally used by Axelrod, and perhaps others, it has usually been a synonym for "Succor Creek." We disagree that the one part of this flora as presently known, which has been age-dated with uncertainty at 16.7 m.y.b.p., is greatly different in age than any of the other florules that comprise the total Succor Creek Flora. In fact, the rocks that have been dated by Evernden and James did not come from the Rockville area (which lies somewhere between localities 1 and 5 as depicted on Fig. 1), but 10 to 15 km south-southeast of the abandoned Rockville post office site or Rockville school, near the junction of U.S. Highway 95 and Succor Creek (near locality 3 or 10, Fig. 1). We consider the Succor Creek Flora to have been accumulated intermittently over a period of one to two million years, in episodically deposited sediments. Because we have repeatedly identified representative cool and warm florules at different levels in the same sections, there is no basis to differentiate the several florules into significantly different age levels on the premise that the cooler floras represent late Miocene age.

MATERIALS STUDIED

It is inferred, from limited geophysical data, that the subsurface on which the Sucker Creek Formation pyroclastics were deposited was an extensive erosion surface of undulating, low-relief topography, developed on volcanic rocks of probable early Miocene age that are possibly time-equivalent to the John Day beds of central Oregon. The upper surface of the Sucker Creek deposits is also extensively eroded and is overlain unconformably by the various rhyolite and basalt flows or clastics of the Idavada Volcanics. The unconformities at the base and the top of the Sucker Creek Formation each represent several million years of exposure and erosion prior to and post-dating the deposition of the Sucker Creek Formation. The best estimates for the total time period for the deposition of the Sucker Creek Formation are between one and two million years, with deposition initiated about 15 or 16 million years ago.

It is evident that various parts of the Succor Creek area were accumulating plant-bearing ash beds intermittently during this one to two million year period. At no point in the area is a continuous stratigraphic sequence exposed that fully represents this time interval. Volcanic activity is episodic in nature and it is probable that most of the time for the Sucker Creek interval is represented by erosional unconformities and diastems where little or no sedimentation of volcaniclastics was occurring in the area. Each of the individual stratigraphic sections exposed within the area documents a specific time interval within the larger Sucker Creek interval but it need not be equivalent in time to other sections within the area. Precise correlation between sections demands comparability in the sequence of identifiable ash beds, preferably coupled with biotic data to substantiate that the sections represent the same or partially overlapping time intervals. These conditions are only rarely met. Given the complexity of volcanic deposition on a topographically variable landscape, one is typically limited to studying the time interval represented by individual sections, ranking them temporally in the longer Sucker Creek interval where data permit. Correlation is even more difficult in the case of exposures of plant-bearing ash in road cuts, gullies, and other sites with limited exposure due to the absence of associated rocks to assist in correlation. Despite such difficulties, it has been possible to trace specific ash beds in outcrop, correlating isolated exposures with measured sections in some cases.

Our postulation that the record of these mid-Miocene volcaniclastic sediments exhibit short-time increments of plant-bearing sediment accumulation and much longer time intervals (gaps) of non-accumulation, is in line with some of the principles summarized by Sadler (1981) and Van Andel (1981). We consider that the Sucker Creek Formation is comprised of a number of discrete episodes of sediment accumulation. This conclusion is based on the nature of the successive vegetation arrays which are represented through the formation by plant fossils of both macro- and microscopic size. The complexities of correlation, coupled with the time significance of diastems and unconformities in the sedimentary record, makes it unrealistic to hope that continuous documentation of the entire Sucker Creek time interval can be achieved. Nevertheless, sufficiently detailed studies of complete sections can be expected to provide a sufficient number of "time samples" to adequately assess the scope of variation in the floristics and vegetation dynamics of the plant communities of Sucker Creek time. Collections for palynologic studies were made from relatively closely-spaced samples from continuous sequences of strata. The sections were measured and described concurrent with sampling. Sedimentary characteristics such as bedding, grain size, texture, and some mineral characteristics were noted. Weathering characteristics, color and lateral continuity and variablity were described. Weathered surface materials and representative slabs and chips of rock from each level and each lithology were examined for larger plant and animal fossils at each sampling site.

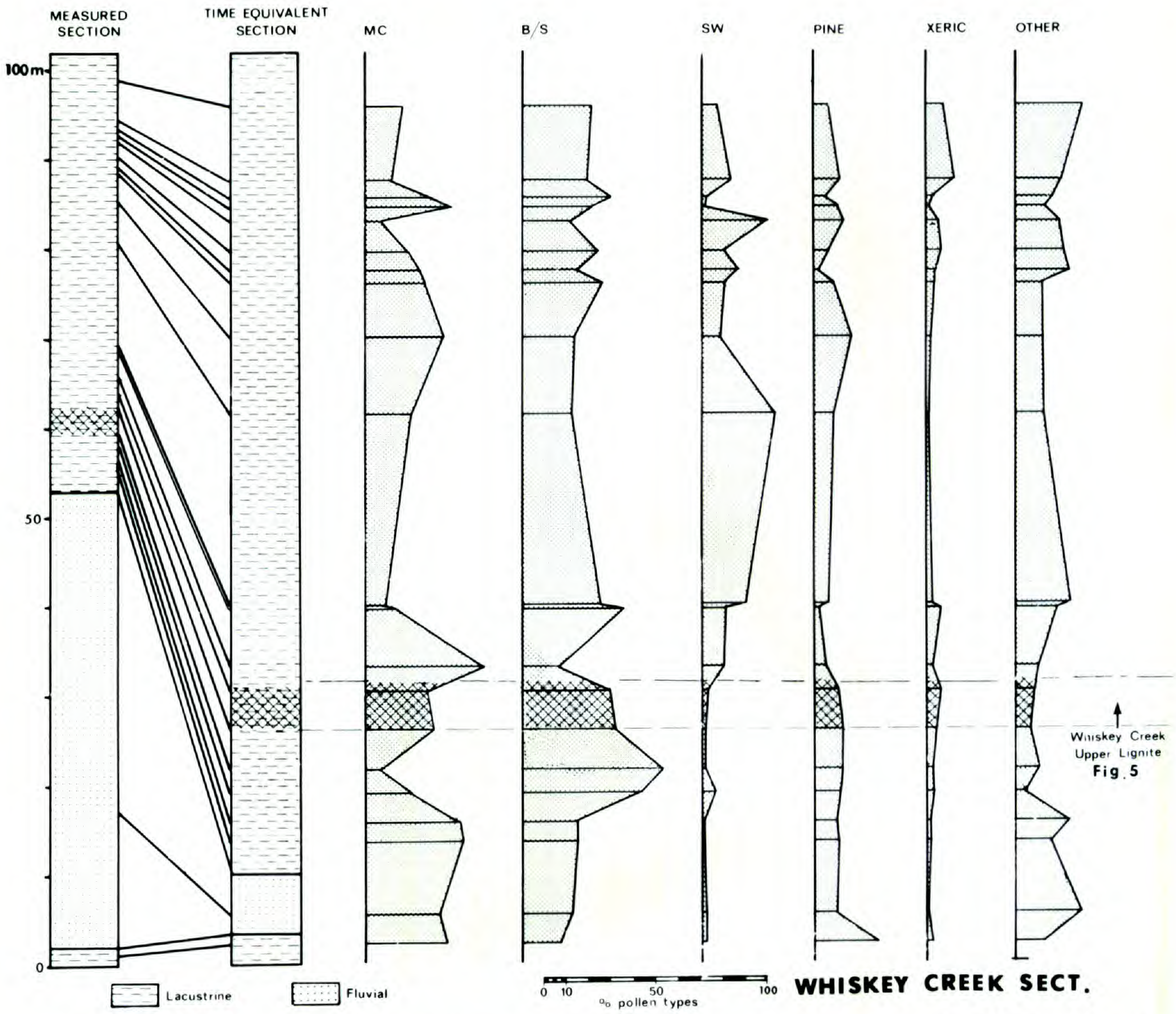


FIGURE 4. Generalized stratigraphy and relative frequency pollen data from the Whiskey Creek section. Classification of fluvial and lacustrine sediments and the rationale for the "Time Equivalent" column are discussed in the text. The following heading keys are used for the paleoassociation pollen profiles: MC, Montane Conifer Paleoassociation; B/S, Bottomland/Slope Paleoassociation; SW, Swamp Paleoassociation; PINE, Pine Paleoassociation; XERIC, Xeric Paleoassociation; and OTHER, Other Paleoassociation. The taxa constituting each paleoassociation are discussed in general terms in the text with a more detailed treatment in Taggart and Cross (1980).

The primary goal of field sampling was to assure that data were limited by the productivity of pollen and spores recovered from the samples rather than by limitations in sampling density. Repeated collections (subsampling or resampling) in subsequent field seasons were commonly made to improve the percentage of productive samples.

PERSPECTIVE

Even with the obvious limitations of the fossil record, all paleobotanists studying Neogene floras from the Pacific Northwest have been struck by the floristic diversity of the Miocene woody vegetation compared with the sagebrush-forb-steppe now occupying the region. The range of Neogene communities probably

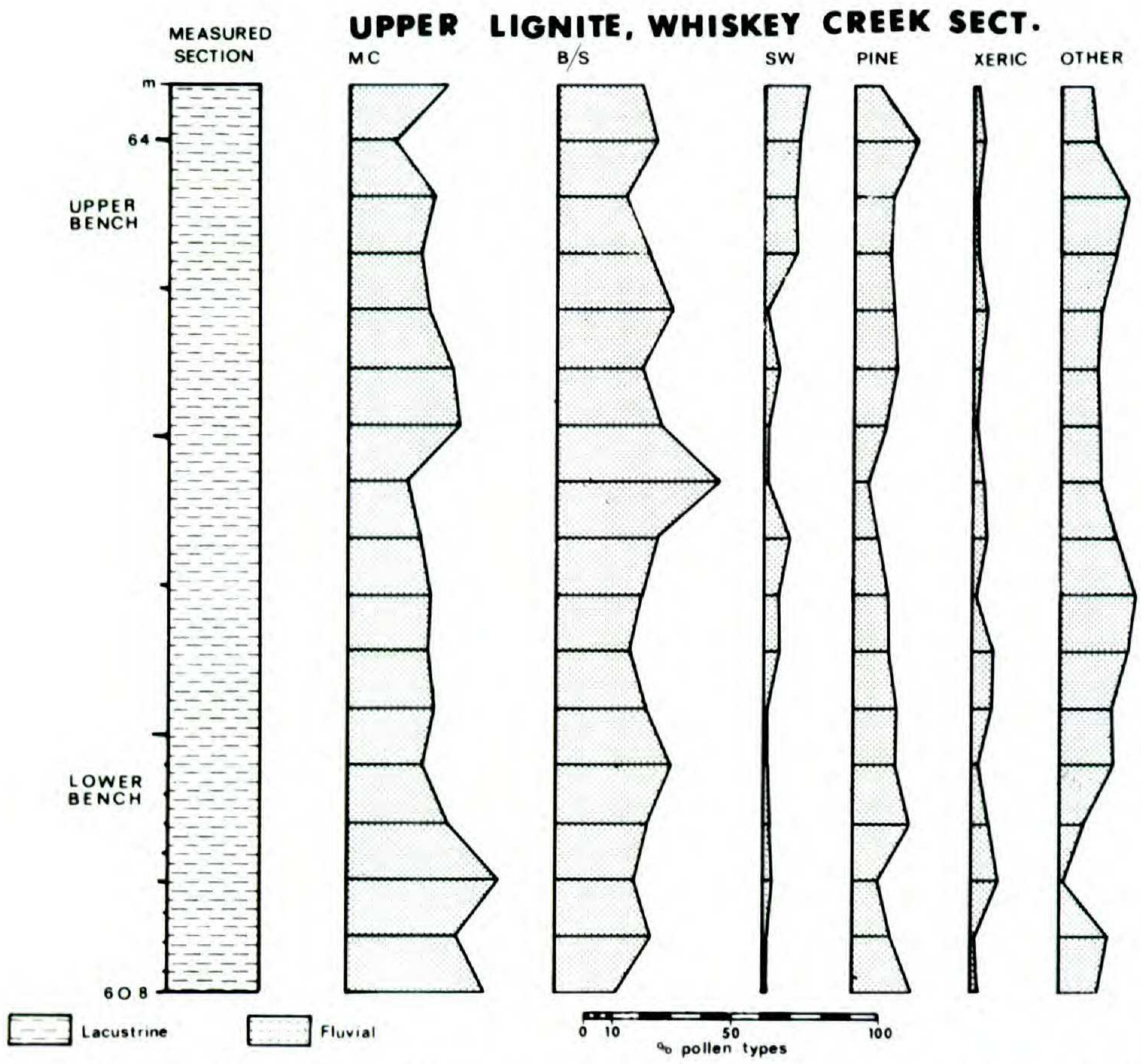


FIGURE 5. Relative frequency pollen data for the Upper Lignite sequence of the Whiskey Creek section. The paleoassociation categories follow the key in Figure 4. The "Lower Bench" and "Upper Bench" designations indicate the general position of the two channel samples representing the Upper Lignite Series in the main Whiskey Creek section profile (Fig. 4).

encompassed a floristic and physiognomic diversity comparable with the extant mesic forests of eastern Asia (Wolfe, 1979), with all of the local variability imposed by historical and site factors.

Paleobotanists have typically been sensitive to the dynamics of hydrologic succession, as these processes are intimately involved with the basins in which fossils accumulate. The work of modern ecologists on disruptive factors such as fire should sensitize us to the certainty of encountering such factors in our fossil assemblages. Similarly, our current understanding of the short-term (10^3–10^4 yr) variability in world climate would lead us to expect that similar variability might have been a factor in the past. Not as obvious, from a uniformitarian perspective, is the nature of regional disruption and widespread destruction of forest vegetation as an inevitable effect of regional volcanic activity on a scale that we have understandable difficulty in comprehending. If the floristic and physiognomic diversity of the ancient forests of this region can so obviously exceed that of the present, so too can the scope of the vegetation dynamics. We have certainly passed well through the survey phase in our study of the Neogene floras of the region and are now attempting, with various approaches, to arrive at an adequate synthesis of the vegetation history of the region. A realistic appreciation of the scope of paleoecological diversity will not confound such an effort; rather it may materially assist in arriving at a consensus derived from many lines of evidence

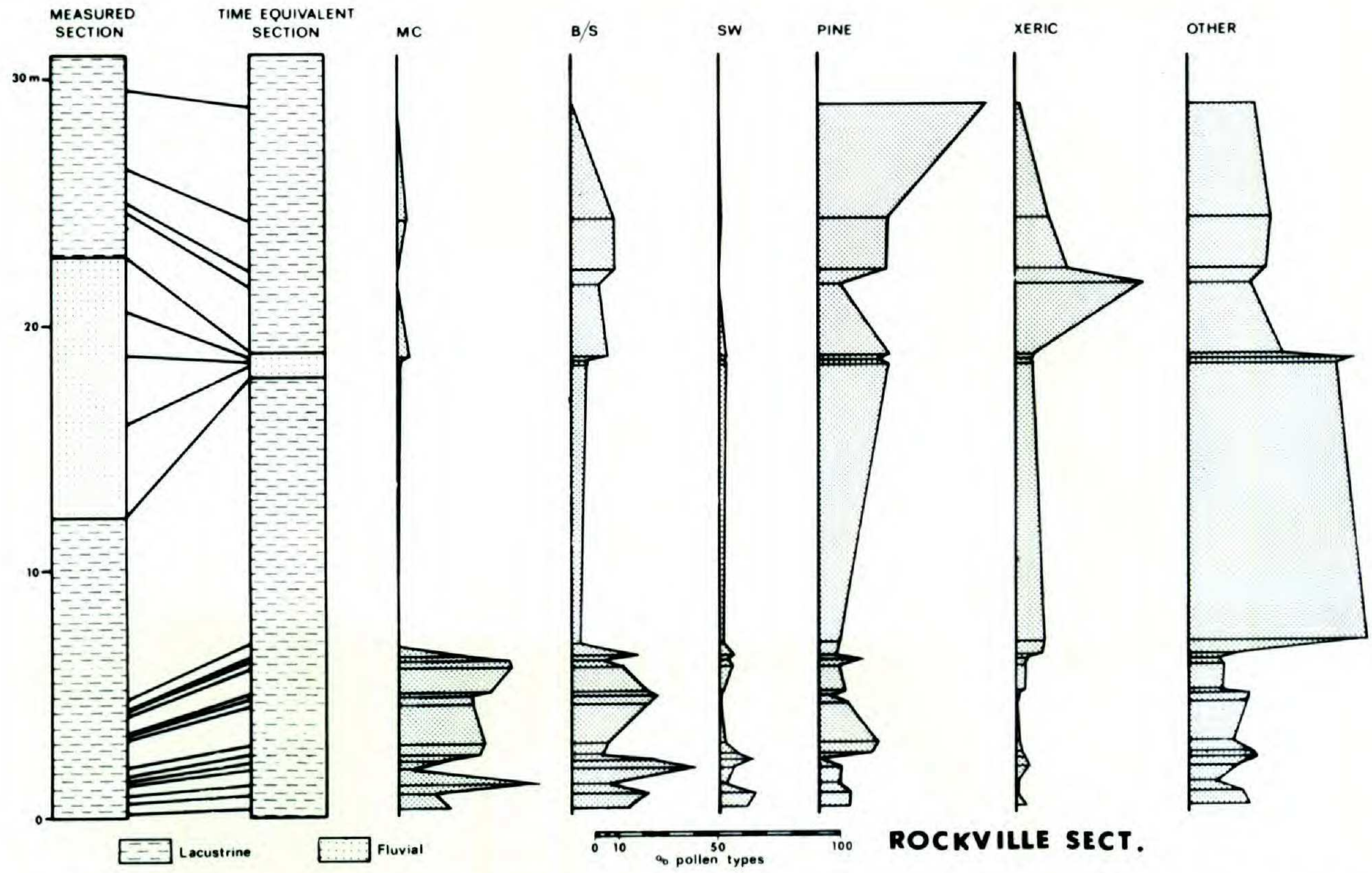


FIGURE 6. Generalized stratigraphy and relative frequency pollen data for the Rockville section. The stratigraphic display and paleoassociation key follows that of Figure 4.

that will permit us to understand rather than simply record the events that have shaped the biotic history of the region.

RESULTS

STRATIGRAPHIC PALYNOLOGY

Pollen diagrams from the Whiskey Creek section (Valley section of Taggart & Cross, 1980), the Upper Lignite of the Whiskey Creek section, and the Rockville, Shortcut, and Type sections are contained in Figures 4–8. These figures incorporate several common elements in a new type of data display that is briefly discussed below.

Measured Stratigraphic Column.—Each figure contains a generalized stratigraphic column summarizing the depositional environment during the period represented by the measured section. Two general sedimentary environments are recognized. Coarse to fine volcanic sandstones and siltstones in this region are considered to represent fluvial depositional environments, and shales, mudstones, and lignites are collectively grouped as representative of lacustrine deposition.

"Time Equivalent" Column.—It is well known that sediments accumulate at different rates in different sedimentary environments, a topic to be further discussed under "Shifts In Community Distribution: Time Factors." Typically thicker deposits of coarser-grained fluvial sediments will accumulate more rapidly than the finer-grained lacustrine sediments. In order to approach a more realistic portrayal of the relative time represented by interbedded fluvial and lacustrine units

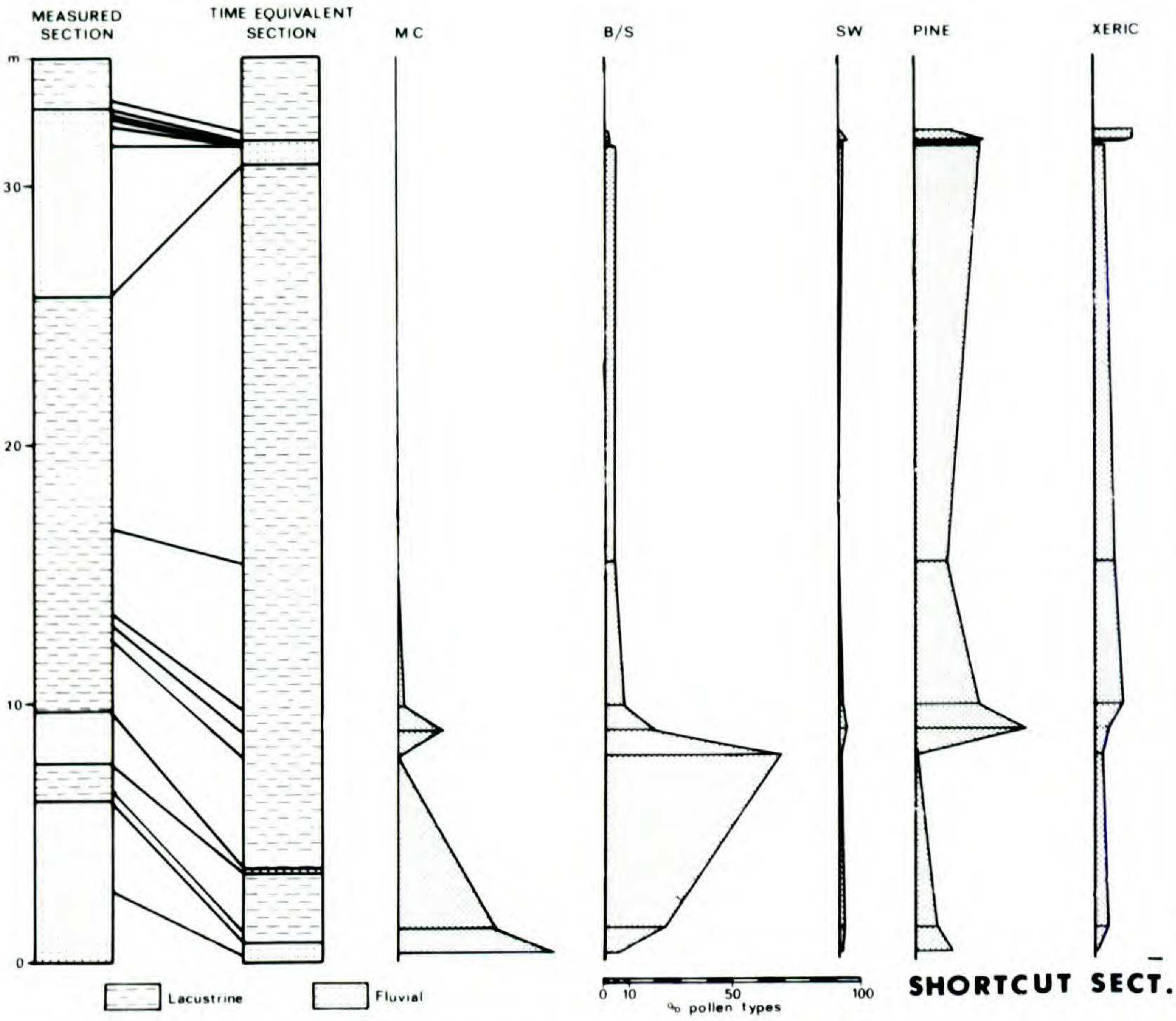


FIGURE 7. Generalized stratigraphy and relative frequency pollen data for the Shortcut section. The stratigraphic display and paleoassociation key follows that of Figure 4.

in a stratigraphic section, the lacustrine units were arbitrarily expanded vertically by a factor of 15 (see discussion under Time Factors: Relative Time Equivalents, etc.), followed by the application of a constant correction factor to all units to re-scale the display (2nd columnar section) to the equivalent of the measured section diagram in each of Figures 4–8. This "time equivalent" column is included to provide a rough approximation of the relative time period represented by the various rock units in each section.

Sample Productivity.—All samples were processed to separate the palynomorphs from the sediments but only those samples yielding sufficient pollen and spores for quantitative treatment are included on the diagrams. Generally 15% to 30% of the samples obtained from each section were productive, with recovery from lacustrine sediments significantly better than from the volcaniclastic dominated fluvial deposits. All samples from the Upper Lignite sequence in the Whiskey Creek section (3 m of organic mudstones, siltstones, and impure lignite) were productive. The positions of all productive samples for each section are plotted on the "Measured Stratigraphic" column for each section as well as on the "Time Equivalent" column.

PALEOASSOCIATIONS

All taxa found during sample tabulations were ultimately recorded in terms of their relative percent contribution to the total pollen and spore count, excluding

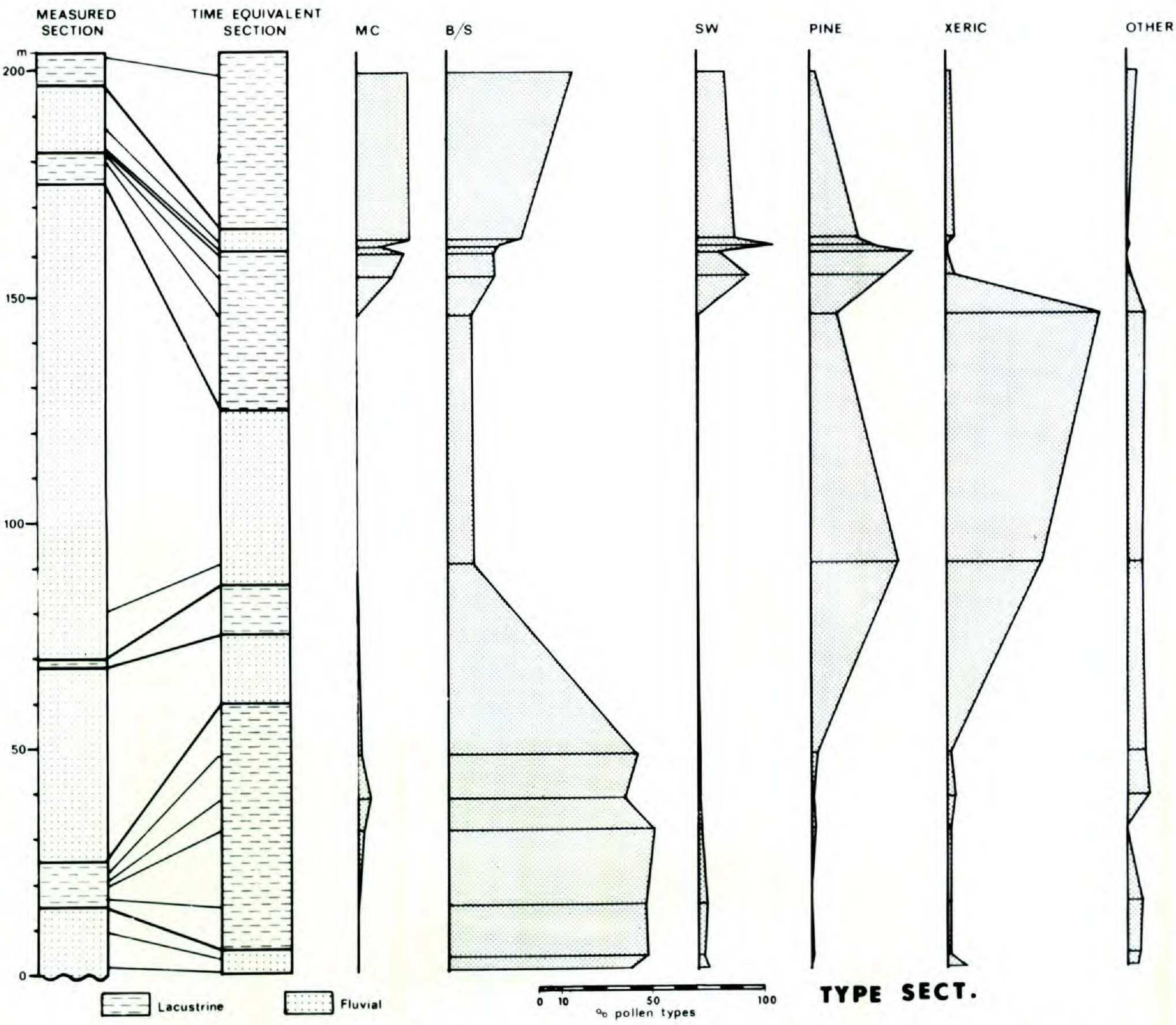


FIGURE 8. Generalized stratigraphy and relative frequency pollen data for the Type section. The stratigraphic display and paleoassociation key follows that of Figure 4.

algal and fungal entities. Over 75 discrete pollen types including 55 genera in 36 families have been encountered in the study sections. The relative frequency pollen diagrams are thus quite complex. The total flora of leaves, fruits, seeds, pollen, and spores from the Sucker Creek Formation now exceeds 50 families.

In order to simplify data display, the various pollen types have been grouped into six generalized "paleoassociations" on the basis of general association of similar source plants in extant communities (Taggart & Cross, 1974, 1980). The Montane Conifer Paleoassociation consists of the pollen of *Picea*, *Abies*, and *Tsuga*, with dominance reflected in this ordering in virtually all cases. All *Pinus* pollen types are grouped into the artificial Pine Paleoassociation based on the wide ecological amplitude of pine species coupled with the difficulty in obtaining precise taxonomic resolution in this complex. The Swamp Paleoassociation is dominated by pollen of the Taxodiaceae, with the pollen of *Typha*, the Nymphaeaceae, and *Potamogeton* included as very minor marsh and aquatic elements. Most of the taxodiaceous pollen is probably attributable to *Glyptostrobus*, which is well-represented by macrofossil material throughout the Succor Creek region.

Taxodium leaf material has, however, been collected at two sites, so a role for *Taxodium* as a possible source plant for taxodiaceous pollen must be considered. The Xeric Paleoassociation includes the pollen of the Chenopodiaceae/Amaranthaceae, Compositae, Gramineae, Leguminosae, Malvaceae, and Onagraceae, plants now associated with somewhat xeric or disturbed habitats. The Bottomland/Slope Paleoassociation is the most diverse, including the pollen of approximately 20 genera of predominantly broad-leaved trees and some shrubs. The important plants of this paleoassociation are *Ulmus, Quercus, Alnus, Carya, Pterocarya, Betula, Acer, Fagus,* and *Juglans*. The sixth category, "Other," is completely artificial and includes the pollen of undifferentiated bisaccate gymnosperms, some unknown but presumably angiospermous pollen types, and undeterminable pollen grains.

The 100 m Whiskey Creek section (Fig. 4) is characterized by oscillations between the Bottomland/Slope and Montane Conifer Paleoassociations. A peak in Swamp pollen near the middle of the section corresponds to the "Valley Plant Beds," an exposure yielding a diverse assemblage of broad-leaved taxa and numerous specimens of *Glyptostrobus*.

The Upper Lignite Series is one of two 3 m lignite and lignitic shale units near the middle of the Whiskey Creek section. The upper unit (Fig. 5) was sampled at 20 cm intervals and indicates a pattern of mild oscillations between the Montane Conifer and Bottomland/Slope elements. There is a gradual trend toward increasing Swamp pollen toward the top of this unit, consistent with the initiation of the Swamp peak in the main Whiskey Creek section.

The Rockville (Fig. 6) and Shortcut (Fig. 7) sections are correlatable throughout most of their thickness and show similar pollen profiles. The basal part of each section is dominated by the pollen of the Montane Conifer and Bottomland/Slope elements but each section shows an abrupt transition marked by the disappearance of the Montane Conifer element and a drop in the number and diversity of Bottomland/Slope pollen. Above this transition the Rockville section shows a pattern of sequential dominance by Other (unknown angiospermous pollen types), Xeric, and Pine Paleoassociations. The Pine maximum at Rockville correlates with the nearby "Pine Locality" where abundant leaf fossils of two- and three-needle pines have been collected.

The Type section diagram (Fig. 8) shows an initial period of Bottomland/Slope pollen dominance, followed by a transition to Xeric and Pine dominance. The upper Type section records an increase in the number and diversity of Bottomland/Slope pollen types, co-dominant with Montane Conifer pollen. The Bottomland/Slope Paleoassociation in the upper Type section is oak-dominated in contrast to elm-dominated spectra from the lower Type section and the other study sections. A leaf bed from the upper Type section is also somewhat atypical in that it is dominated by *Ulmus* and *Salix* and contains leaves of *Carya* and *Populus* cf. *pliotremuloides*, the only Succor Creek leaf records for these latter two taxa.

We have also studied the Rocky Ford section, an 11.2 m lacustrine unit outcropping across Succor Creek about 375 m to the west of the base of the Type section exposure. If dips are consistent across the Succor Creek valley, field measurements indicate that the top of the Rocky Ford sequence correlates to within 2 m of the base of the Type section. Two productive samples were recovered from the Rocky Ford sequence. Both are similar in composition, averaging 39% Montane Conifer, 47% Bottomland/Slope, 1.5% Swamp, 9% Pine, 1% Xeric, and 2.5% Other pollen. Palynologically, the Rocky Ford samples are indistinguishable from those of the Whiskey Creek and lower Rockville and Shortcut sections but are quite different from the Bottomland/Slope dominated spectra of the basal Type section. Thus, although structural indications point to only a slightly earlier age for the Rocky Ford sediments, relative to the basal Type section, the possiblity of faulting, a diastem or an unconformity must be considered.

SUMMARY OF DATA DISPLAYED IN FIGURES 4–8

Three main pollen/spore assemblages have been differentiated in the sections studied and have been plotted on a time equivalent base.

1. *Co-dominance of Montane Conifer and Bottomland/Slope Paleoassociations.*—There is often considerable variation in the relative importance of these two elements where they co-occur. Swamp pollen may increase to significant levels at times. Pine and Xeric elements are typically minor. This assemblage is characteristic of the entire Whiskey Creek section, the lower Shortcut and Rockville sections, the Rocky Ford section, and the upper Type section.

2. *Dominance by the Bottomland/Slope Paleoassociation.*—Bottomland/Slope element ranging from 75% to 90% for an extended period of time; Montane Conifer pollen virtually absent, and other elements are of minor importance. This is an assemblage that has been found only in the lower Type section and at several intervals in the lower Devils Gate section.

3. *Xeric/Pine Assemblage.*—Pollen record dominated by Xeric and Pine Paleoassociations, including the "Other" category when the latter is dominated by pollen of plants of unknown but presumably herbaceous affinities. Montane Conifer pollen typically lacking, with Swamp pollen at low levels. Bottomland/Slope representation is typically low in both numbers and diversity.

DISCUSSION

A CONCEPTUAL FRAMEWORK FOR ECOLOGICAL RECONSTRUCTION

The Clements (1916) concept of "climax" vegetation is simple in its most basic form, i.e., the vegetation type of a region that exists in equilibrium with the prevailing climatic regime. However, the concept becomes complex when applied to real plant distribution. Most ecologists now recognize that the climatically controlled vegetation of any region is in reality a complex mosaic with the distribution of community types controlled by a wide variety of factors. These include elevation, slope exposure and other edaphic factors, microclimatic amelioration, the biotic potential of the region, past community distributions, and the degree and timing of events acting to disturb or disrupt community structure. Documentation of the nature of the climax mosaic is complicated throughout much of the northern hemisphere because many vegetation types may not have reached equilibrium since the most recent Pleistocene glacial maximum. Recent data also suggest that, on the scale of the centuries, climate is not stable. Furthermore, the size of natural communities, coupled with disturbances such as fire and human intervention, may preclude the "steady state" inherent in the climax concept (Bormann & Likens, 1979). Shugart and West (1981) note that "forest ecosystems are dynamic entities that may not be static in either time or space. Many of our concepts are based on the hope that if a forest is left alone it will gradually return to its natural state." They also note that, ". . . 'succession,' 'wilderness,' 'virgin forests,' and 'climax forests,' are all concepts that appeal to the basic notion that forest systems should approach some equilibrium state with time . . . ." They state that, ". . . research indicates that forests in highly disturbed landscape may remain in perpetual state of effective non-equilibrium and that if the scale of disturbance is large, then the amount of land required to absorb the effects of the disturbance is also large" (p. 647).

Paleobotanical analysis of Tertiary floras is directed toward understanding the floristics of fossil assemblages and the type and distribution of the ancient plant communities and to utilize the data to reconstruct the climate of a region. This has been the case with the Neogene floras of the Pacific Northwest where two principal approaches to paleoclimatic reconstruction have been utilized. In the paleoecological approach, typified by such works as that of Axelrod and Bailey (1969), an attempt is made to reconstruct the nature of thermal conditions that controlled floras by analysis of the ecological affinities of the fossil plants. Others (e.g., Wolfe, 1978) utilize leaf physiognomy as a climatic indicator in an attempt to avoid limitations in our understanding of the floristics of an assemblage and the unknown factors of ecological constancy of taxa with the passage of time.

These two approaches have yet to converge on a consensus regarding the pattern of Neogene paleoclimatic dynamics. It is not our intention here to argue for one approach or the other but there is an *a priori* assumption inherent in both approaches, that the floras under study represent a mosaic of vegetation types in a steady state or "climax" equilibrium with climate. If this assumption is not the case, then the flora under study cannot provide a reliable indication of the climate under which the flora was developed. It is also assumed that changes in climate, which would shift the nature of this equilibrium, are not operating within the time period represented by a single flora but can be resolved by comparisons between floras of different ages. Such conditions may pertain for some fossil plant assemblages, but it is our contention that many Neogene floras of the Pacific Northwest probably do not meet the conditions required to make the assumption that a relatively steady state equilibrium between vegetation and climate existed in such floras.

The preservation of the fine suite of floras in the region is due to an interval of intense volcanic activity throughout the area that has no parallel in historical human experience. It is unrealistic to assume that such vast outpourings of volcanic debris would have uniformly preserved samples of climax vegetation. If any particular area on the earth's surface today were subjected to such massive disturbance, a modern ecologist would expect the vegetation of the region to reflect the magnitude and episodic nature of the disturbances with a variety of communities reflecting successive seres leading to varying degrees of climax equilibrium with the prevailing climatic regime. In such an area, relative stability in vegetation distribution might well be the exception rather than the rule. Our studies indicate that this appears to have been the case in southeastern Oregon and southwestern Idaho during Sucker Creek time. Our data (Fig. 9) do provide indications as to the scope of the climax vegetation mosaic for the region but also record a number of disturbance factors that have served to disrupt or modify the distribution of plant communities including:

1. Hydrologic succession, involving the formation, eutrophication, and infilling of ponds and lakes, initially formed largely by damming due to ash falls, lava flows, and possibly by earthquake induced landslides.
2. Post-disturbance succession of at least two types:
   A. Disruption of vegetation by ash falls, gas venting, and mudflows associated with local and regional volcanic activity.
   B. More localized forest disruption by fire.
3. Cliseral shifts in vegetation distribution induced by thermal oscillations of small magnitude, possibly coupled with shifts in the precipitation regime, which are sufficient to mask any long-term trends in climatic change through Sucker Creek time.

THE NATURE OF SUCCOR CREEK CLIMAX VEGETATION

The macrofossil record for the Succor Creek Flora indicates a diverse broad-leaved forest with a restricted representation of montane conifers (spruce, fir, hemlock, and pine), identified by a small number of seeds, presumably carried into the basin by streams draining higher elevations. The presence of several genera whose extant representatives are sensitive to frost, such as *Cedrela, Persea,* and *Hiraea,* led Graham (1965) to suggest that the Succor Creek assemblage represented a warm temperate forest in which frost was rare and of short duration. The very strong deciduous aspect of the Succor Creek Flora was supported by Axelrod (1968). He mapped the Succor Creek Flora as part of a "slope forest" unit and created an eastward salient on the map of the distribution of the unit (Axelrod, 1968, fig. 7B) to accommodate the Succor Creek macrofossil data.

Palynological investigations of the flora and additional macrofossil studies of many more localities at stratigraphically oriented sites indicate that classification of the Miocene regional vegetation in the Succor Creek area as primarily broad-leaved forest is inappropriate and that greater attention must be given to the role of montane conifers in reconstruction of undisturbed Succor Creek vegetation. The pollen of spruce, fir, pine, and hemlock, assumed to have variable significance in montane forests, is routinely encountered. This discussion of climax vegetation will exclude consideration of pine. Pine pollen can be dispersed over a very large geographic area and may be carried upward or downward from source areas in large amounts (King, 1967). Leopold (1964) suggested that pine pollen percentages bear little relationship to the importance of pine in standing timber and virtually all studies of modern pollen rain support the cosmopolitan distribution of pine pollen in regions where pine is present. Our own studies of a transect of five stations in the Mt. Mitchell area of North Carolina (Table 1) show pine pollen percentages ranging from 7% to 11%, irrespective of whether pine was present in the forest vegetation surrounding the collection site. Pine pollen is invariably present in Succor Creek pollen preparations but, with the exception

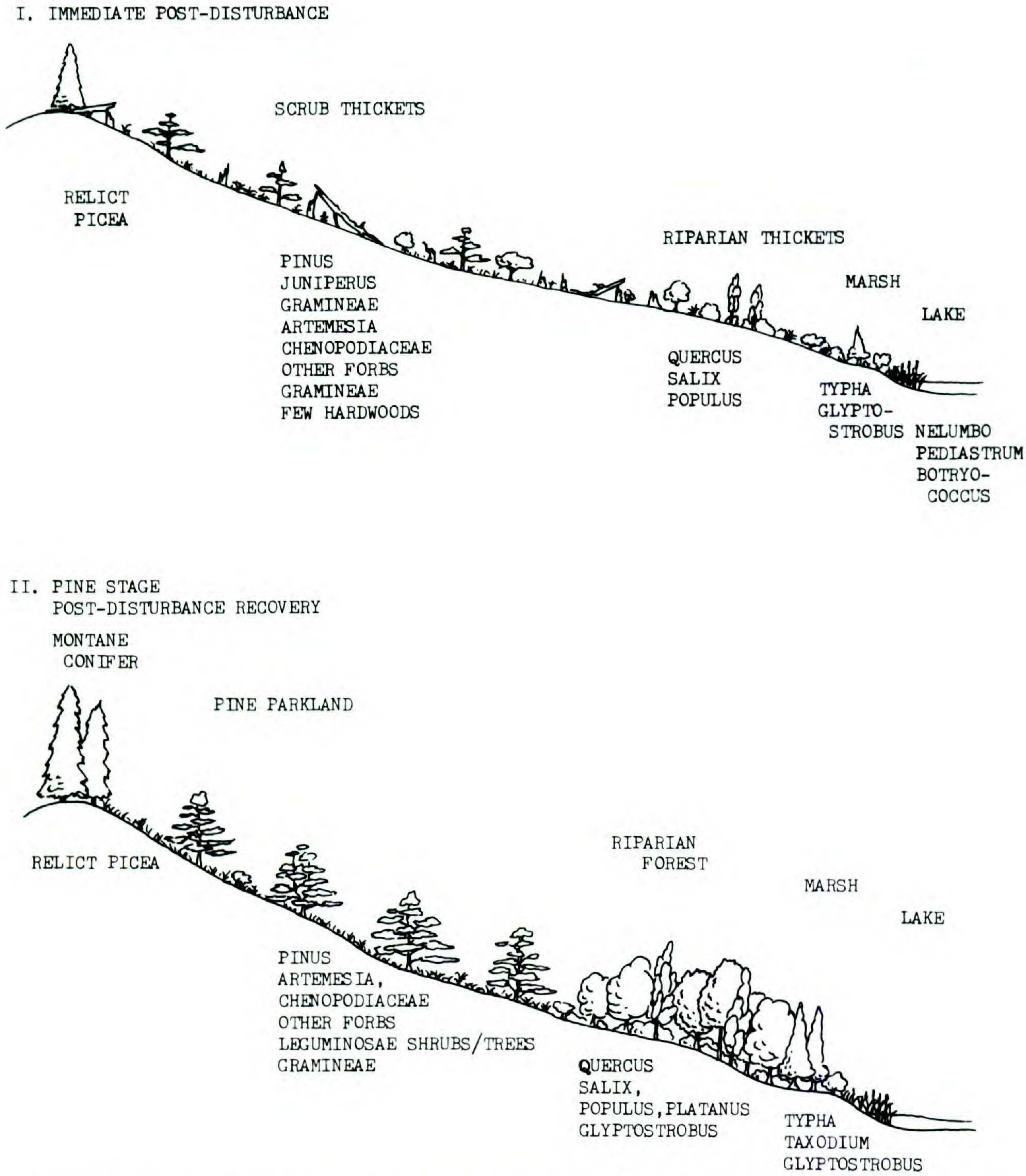
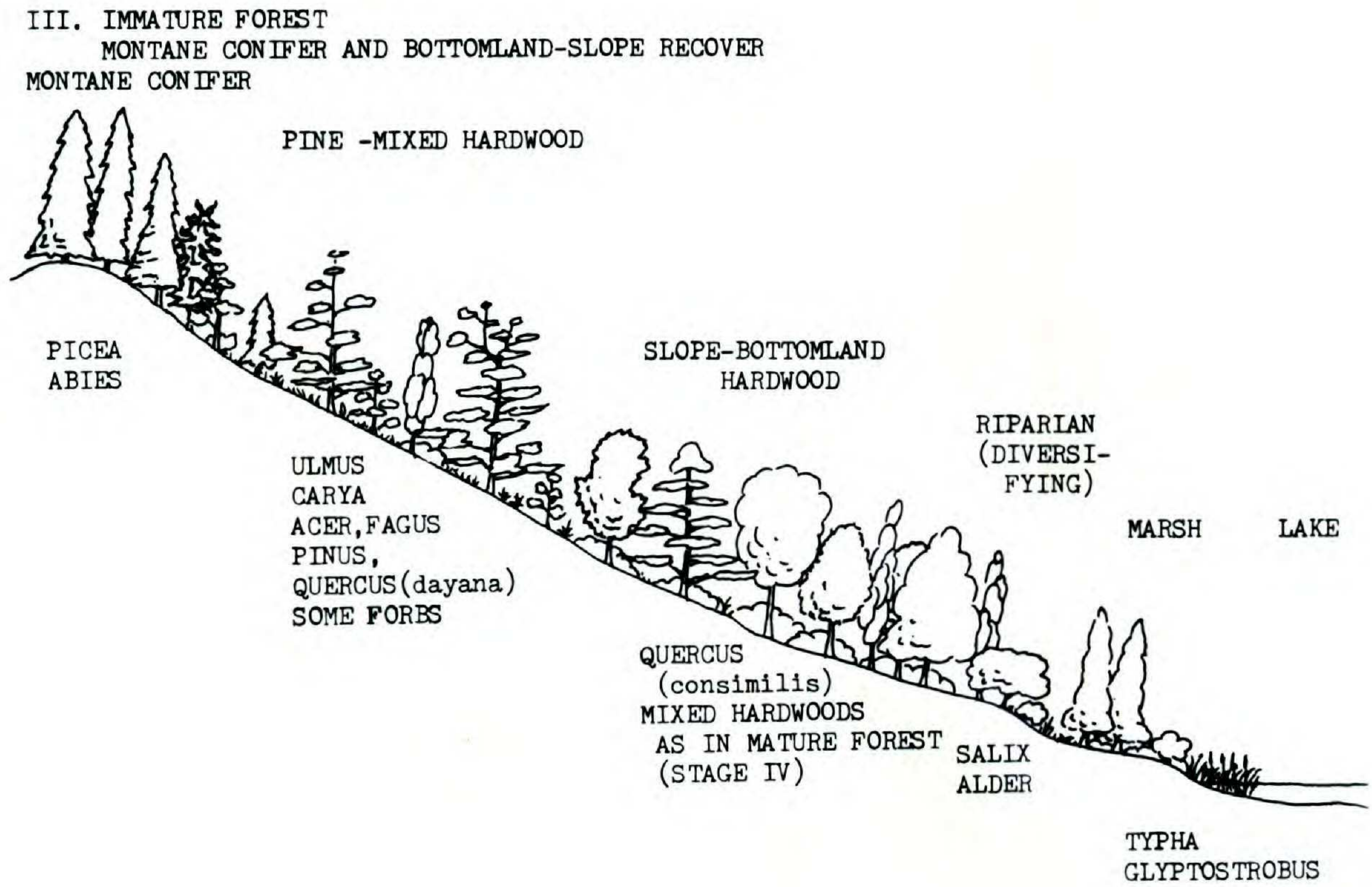
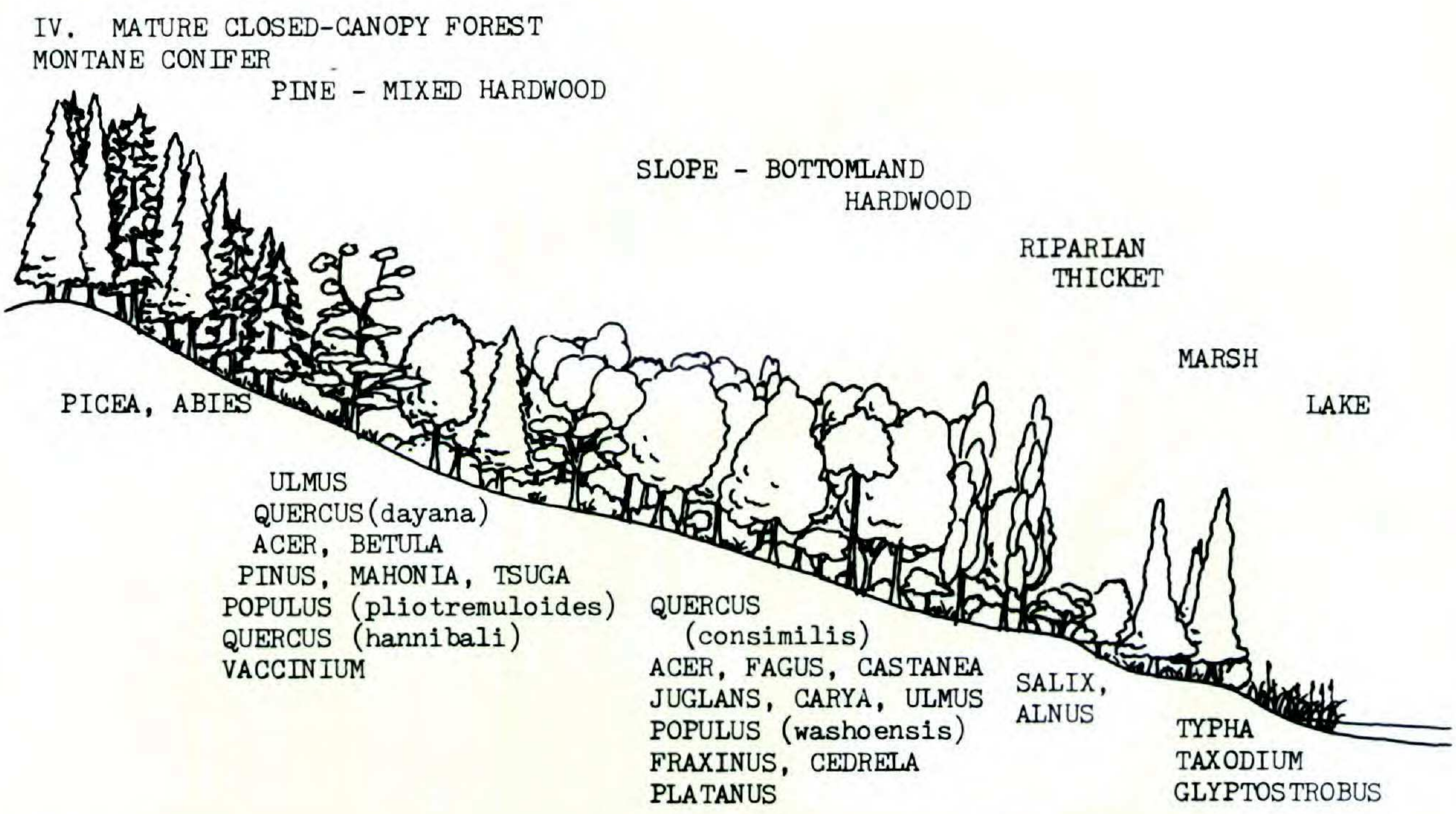


FIGURE 9. Generalized reconstructions of Succor Creek vegetation distribution at various stages following massive volcanic disturbance. I. The vegetation array shortly after disturbance with a limited riparian assemblage surrounding the depositional basin with most of the area dominated by a grass-forb complex with seedlings of trees and shrubs becoming established. II. The "Pine Stage" in the recovery sequence with a more diverse riparian forest in the lowlands and the development of a pine-parkland on surrounding slopes. III. A late post-disturbance stage with progressive development of

of its marked presence in the post-disturbance vegetation, the pine pollen component can be considered as background, derived from trees sparsely scattered through the forests at various elevations.

The pollen of spruce, fir, and hemlock, which we have previously grouped together as the Montane Conifer Paleoassociation (Taggart & Cross, 1980), is significant however. Although Graham (1965) was the first to note the presence





lowland forests, successional deciduous forests on low slopes (possibly with extensive pure stands of *Carya* and *Liquidambar*), and re-development of the montane conifer forests at higher elevations. IV. This portrays essentially "climax" or steady-state community distribution with well-developed conifer forests on the low hills, grading into broad-leaved forests on the lower slopes and into the bottomlands surrounding the basins of deposition.

of these conifers in the Succor Creek pollen record, the data did not influence his interpretation of the flora as warm temperate. We have noted (Taggart & Cross, 1980) that, where present, the pollen of the Montane Conifer Paleoassociation averages 25%, reaching peaks of 50% to 60% in some sections. To account

TABLE 1. Modern pollen rain, classified according to the Succor Creek Paleoassociations (Taggart & Cross, 1980) for five stations in the area of Mt. Mitchell, North Carolina (U.S.A.).

		Pollen Spectrum				
Elevation	Vegetation	Montane Conifer	Bottom-land/ Slope	Pine	Xeric	Other
2,013 m	Fir-spruce forest	26	53	11	10	0
1,739 m	Deciduous forest, spruce common	10	69	11	9	1
1,586 m	Deciduous forest, spruce present	4	78	14	4	0
1,452 m	Deciduous forest, hemlock present, spruce erratic, scattered pine	4*	76	7	13	0
1,037 m	Deciduous forest, scattered hemlock, scattered pine	5*	80	9	6	0

* Hemlock dominated.

for this significant montane conifer component we have interpreted the vegetation as having been developed on a topographically diverse landscape, with low-slope gradients, under a cool but highly equable climatic regime. Small thermal oscillations would have resulted in minor elevational shifts in the ecotone between the conifer and broad-leaved forests, which, when coupled with low-slope gradients, would result in pronounced changes in the distance between the ecotone and the depositional basin. These small elevational but widespread areal shifts would produce the pronounced inverse oscillations in the relative representation of the two paleoassociations in the pollen record.

Our reconstruction is greatly influenced by the levels of Montane Conifer pollen noted in our spectra. Our interpretation might be viewed as overstating the importance of pollen that some consider to have been carried into the basin from a considerable distance (e.g., Axelrod, 1965, p. 169). Such a view is often based on an appreciation of the wide dispersal range of pine pollen and the supposition that the pollen of other conifers with vesiculate pollen must behave similarly. Leopold (1964) noted that spruce pollen percentages are roughly comparable to the relative representation of the species present in area forests and that fir pollen is greatly under-represented. King (1967) noted that the proportion of spruce in the total pollen rain diminishes very quickly outside of the area of spruce occurrence in the Sandia Mountains of New Mexico and similar results were obtained by Dixon (1962) and Maher (1963) from the Sangre de Cristo Mountains of New Mexico and the San Juan Mountains of Colorado. Potter and Rowley (1960) noted the virtual absence of spruce pollen in the modern pollen rain of the San Augustin Plains of New Mexico, despite the presence of a 400 hectare stand of spruce located approximately 22 km from the border of the drainage area. They state that any significant amount of spruce pollen in a sedimentary profile would indicate the near presence of spruce.

In one of our own studies, used here to typify pollen dispersal in a more densely forested region, a collection of moss polsters was made at five stations on Mt. Mitchell in the Blue Ridge Mountains of North Carolina. The dominant regional vegetation is of the Mixed Mesophytic Forest Association with spruce-fir montane forests developed progressively above 1,500 m. The results, with pollen taxa grouped into associations comparable to the paleoassociations used in our Succor Creek study, are shown in Table 1. At the highest station, just below the Mt. Mitchell summit (2,013 m) in a closed canopy fir forest (*Abies fraseri*) with scattered spruce (*Picea rubens*), Montane Conifer pollen reaches 26%, roughly equivalent to the *average* representation of the comparable paleoassociation in the Succor Creek record. The Montane Conifer assemblage drops to 10% at 1,739 m, despite the fact that spruce is a common forest component at this level. At 1,586 m and lower on the slopes, the Montane Conifer element drops to quite low percentages with the majority at lower elevations composed of hemlock pollen in forests where hemlock is commonly present. Even at the summit in a closed-canopy conifer forest, the conifer pollen rain is diluted by the massive influx of pollen derived from the extensive regional deciduous forest.

Given the 25% average representation of Montane Conifer pollen in the Succor Creek record, with peak spectrum values of 50–60%, long-range transport of this pollen is simply not to be expected. The megafossil record makes it clear that the vegetation surrounding the basin was a broad-leaved forest, yet Montane Conifer pollen levels are comparable to and typically exceed those noted in the conifer forest in the North Carolina collections. The relatively high conifer pollen levels in the Succor Creek Flora indicate massive pollen rain from a regional spruce-fir forest that is diluted by the deciduous forest pollen produced locally at lower elevations in the valley systems.

A flora under study from the nearby Reynolds Creek watershed of Idaho provides additional collateral data bearing on the question of the Succor Creek thermal regime. The Reynolds Creek deposits are considered equivalent in age to the Sucker Creek and yield pollen spectra comparable to those from Whiskey Creek, lower Rockville and Shortcut, Rocky Ford, and upper Type sections, including Montane Conifer Paleoassociation pollen values from 0 to 24% (mean of 7.2%). Diatoms we have recovered from our Reynolds Creek samples are currently under study by J. Platt Bradbury, of the U.S. Geological Survey, and appear to indicate the presence of a cool, shallow-water environment (Bradbury, pers. comm., 6 January 1981). We have also isolated zygospores of *Mougeotia* (Zygnemataceae) from these samples. van Geel and van der Hammen (1978) note the recovery of *Mougeotia* zygospores from the Quaternary of the Colombian Andes and its modern occurrence at sites between 2,100 and 4,500 m. Hoshaw (1968) noted that optimum growth temperature for the genus falls between 10° and 15°C. Round (1965) cited numerous occurrences of *Mougeotia* in algal communities of ponds, lakes, and rivers with most examples drawn from sites in cool to cold climates. Cool, shallow-water habitats suggested by fossil algae in the Reynolds Creek strata are consistent with our climatic reconstruction but such conditions would be quite restricted seasonally if the climatic regime were warm temperate.

Axelrod (1976) presented a large body of evidence re-interpreting the significance of montane conifers as "sub-alpine" forest indicators. Macrofossil evidence of genera such as *Abies, Picea, Pseudotsuga, Tsuga,* and many species of *Pinus* has led to suggestions of high altitude source areas supporting sub-alpine conifer forests with isolated needles and seeds being transported relatively long distances to lowland basins of deposition. Axelrod argues persuasively that fossil remains of such conifers represent diverse conifer-hardwood forests located relatively close to the lowland depositional basins and that where sufficient relief was present, such mixed forests would become ecotonal to true sub-alpine conifer forests. Our data support his generalized reconstruction with perhaps even stronger emphasis on the role of conifers in the regional vegetation. In our flora, the lack of geological evidence for alpine topography, coupled with the very high percentage of montane conifers, would suggest that extensive conifer forests were developed at moderate elevations throughout the area, probably with a variety of ecotones between the montane conifer forest(s) and the predominantly broad-leaved forests of low slopes and lowlands (Fig. 9-IV). This is consistent with the pollen records from the Whiskey Creek, lower Shortcut and Rockville and the Rocky Ford sections, and the upper part of the Type section. A more detailed description of the diverse communities making up the lowland deciduous forest is given in an earlier publication (Taggart & Cross, 1980). The Montane Conifer element is essentially lacking in the spectra from the lower Type section, a matter of possible significance to be discussed within the topic of cliseral changes.

HYDROLOGIC SUCCESSION

The various paleoassociations that are identified from the pollen record of the Whiskey Creek, lower Rockville, and lower Shortcut sections show patterns of interaction indicative of shifts in the mosaic of vegetation types dominating the landscape during Sucker Creek time. One such event is identified by the pronounced peak in the Swamp Paleoassociation (largely pollen of the Taxodiaceae) in the Whiskey Creek section (Fig. 4) from thinly laminated shales of probable lacustrine origin. Several types of algae (*Botryococcus, Pediastrum,* and diatoms) are evidence for the presence here of ponds or lakes, formed by impoundment of streams by extrusives or mud or ash flows. The most likely explanation for the swamp pollen peak in this section is the occurrence of a hydrologic succession linked with the eutrophication of the pond or lake. In this case the swampy margins of the aging lake supported increasingly extensive stands of *Glyptostrobus* and possibly *Taxodium.* Ultimately the lake basin filled with sediments, including the peats, and the old lake area gradually became a bottomland habitat with the penecontemporaneous decline in the abundance of *Glyptostrobus* pollen transported to the basins of deposition. This example of hydrologic succession may also provide a rough calibration of the time interval represented by the shales of the Whiskey Creek section and, by inference, a rough guide to the sedimentation rates for other sections in the area. The process of eutrophication can require as little as a century for a small lake and up to many thousands of years for large lake systems. As there is no available geological evidence supporting the existence of very large lakes in the Succor Creek area, it is reasonable to assume that the Whiskey Creek lake(s) was of limited size and may have filled in within a thousand years or so. If this was the case, the 50 m shale and siltstone sequence in the upper part of the Whiskey Creek section was probably accumulated within a very short time, geologically, i.e., a few thousand to ten thousand years. Swamp pollen peaks are noted in most sections but they are of less magnitude and shorter duration than that of Whiskey Creek. This indicates that most lakes or ponds were of small size. It is possible that some may have been prematurely drained by breaching of the containment feature (lava dam, mud flow, ash fall, etc.), which resulted in termination of the swamp environment and a shift back to bottomland forest.

The relationship of the Swamp pollen peak in the Whiskey Creek pollen diagram to the sedimentary record raises some interesting questions regarding the use of sedimentary data in paleoecological reconstruction. The Upper and Lower Lignite Series represent the two principal periods in Whiskey Creek time where direct sedimentary evidence exists for the presence of peat swamps. Yet the Swamp pollen profile indicates that during the period where the sampling site was accumulating peat, the overall level of Swamp pollen was comparatively low. Only later in time, when the sampling site was accumulating mud (that represents the overlying shales now termed the Valley Plant Beds), does the Swamp pollen level rise to a peak in excess of 30%. Although most Swamp pollen peaks in the study sections are of smaller magnitude than the Whiskey Creek example, it is quite common to find that a Swamp peak does not always correlate to the same level in a section where one finds the best lignite development. The presence of lignites is clearly not *prima facie* evidence of maximum extent of swamp development as evidenced by these pollen records of the Swamp Paleoassociation in the Succor Creek area.

In excess of 95% of the pollen of the Swamp Paleoassociation is that of the Taxodiaceae, either *Glyptostrobus* or *Taxodium*. There can be little doubt that both plants were intimately associated with environments where peat was accumulating. The Rocky Ford section has excellent leaf impressions of *Glyptostrobus* and some *Taxodium*. An organic zone at the Devils Gate section (Fig. 1, loc. 9) is dominated by leaves and branches of *Glyptostrobus*. Virtually all preserved fossil stumps in the Succor Creek area are rooted in lignites or organic shales and invariably are assignable to the Taxodiaceae, based on thin-sections of the wood. An excellent "fossil forest" of this type is present in the upper Rockville section.

Lack of correlation between Swamp pollen peaks and organic deposition is rather surprising but an explanation may be found in the nature and extent of the Succor Creek swamps. Given the variable topography assumed for the landscape, the most likely site for swamp development would be shallow lake margins and headwaters. It is possible that most of these swamps were of limited geographic extent and rather patchily distributed over the landscape, based on the relatively minor contribution of Swamp pollen to most pollen spectra. In the case of the Whiskey Creek lignites, although peats were accumulating at the sample site, the swamp was too small for the input of Swamp pollen to override the massive pollen influx from the surrounding broad-leaved and coniferous forests.

The presence of lacustrine shales of the Valley Plant Beds overlying the lignite indicates a probable increase in lake level, which converted the old swamp to an open-water site where mud accumulated over the peat. The cause of such an increase in water level is conjectural but the overall Whiskey Creek floristic record shows no evidence of profound disturbance by volcanic activity, so ash fall or lava dams are unlikely. However, an earthquake induced landslide could have dammed the valley, increased the water level (Adams, 1981) and formed an open-water environment at the sampling sites. The surrounding areas, previously supporting bottomland forest elements, would have become flooded and more extensive areas of swamp could have spread around the expanded lake margin. In this case, the increased area of swamp development resulted in larger inputs of Swamp pollen and hence the pollen peak in the Valley Plant Beds. Lignites and other organic sediments in interior continental deposits certainly record the presence of swamps but, in any specific section, they need not signify the period of maximum swamp development in the region as a whole.

SHIFTS IN COMMUNITY DISTRIBUTION

A major dynamic feature of the pollen diagrams of the Whiskey Creek, lower Rockville, and lower Shortcut sections is the interaction in relative frequency of the Bottomland/Slope and Montane Conifer Paleoassociations. These pronounced oscillations raise two primary questions: to what extent did mutual oscillations occur in the major components of the source vegetation, and what mechanisms exist to explain changes in the nature of the source communities?

Our Succor Creek pollen data are tabulated as relative frequency pollen diagrams made up of individual pollen spectra, each spectrum representing the total pollen tabulated for a sample. Within each spectrum the contribution of each taxon is expressed as a percentage of the total pollen count for that sample (Taggart & Cross, 1974). The paleoassociation percentages simply represent the aggregate of percentages for all taxa assigned to a specific paleoassociation. Essentially the paleoassociation curves constructed from these percentages are analogous to curves for individual taxa although they tend to be highly damped because each paleoassociation contains more than a single taxon. This damping is particularly true in the case of the Bottomland/Slope Paleoassociation since it is the most inclusive of the categories. The primary limitation of a relative pollen diagram is that if there is a major shift in the pollen contribution of any major component of the spectrum the relative frequency of the remaining components must change, since all data are expressed as a percentage of total pollen. The result may be a change in the expressed percentage of some components of a spectrum without changes in the importance or distribution of the source plants.

Such an anomalous interaction is most likely to occur in the case of a genus such as *Pinus*, which produces disproportionately large quantities of pollen with excellent aerodynamic and hydrodynamic characteristics for dispersal and high durability. Pine may be present as trees sparsely scattered in a forest, yet may represent 10% of the pollen record. For illustration, let us assume that the remaining 90% of the pollen rain is made up equally of the Bottomland/Slope and Montane Conifer Paleoassociations, each contributing 45%. Due to some circumstance, the percentage of pine pollen might increase to 20%. This could be due to a number of factors, a slight increase in population levels of pine, establishment of even a few trees somewhat closer to the basin, etc. None of these factors need imply any significant increased importance in the contribution of pine in the local vegetation and the composition and distribution of other forest elements would remain essentially unchanged, yet the Bottomland/Slope and Montane Conifer pollen levels would each drop to 40% due to the greater input of pine pollen. It should be noted, however, that although the drop in the other paleoassociation percentages is meaningless "noise" relative to their composition and distribution, the increase in the level of pine pollen does reflect some real event relative to pine populations or distribution even though it might be marginally resolvable in terms of regional phytosociology.

A similar situation occurs with alder pollen in some samples. *Alnus* probably occurred in thickets marginal to ponds, lakes, and wetlands and, when the plants were abundant locally, their pollen may have dominated a specific spectrum, enhancing the Bottomland/Slope percentage at the expense of other paleoassociations. Such single taxon biases are usually apparent and their effect may be mitigated by excluding the suspect taxon from the pollen sum when assessing the dynamics of the remaining components.

In spite of all such considerations, the Whiskey Creek, lower Rockville, and lower Shortcut sections are characterized by pronounced oscillations or shifts between the Bottomland/Slope and Montane Conifer Paleoassociations. Such oscillations are not single taxon phenomena but represent coordinated shifts in the representation of entire paleoassociations, which are, by their nature, damped due to the inclusion of multiple taxa. Although it may be argued that the relative response of the individual paleoassociations is linked, due to the nature of relative pollen diagrams, such a view overlooks essential realities in the nature of plant community distribution. Climax or subclimax forest communities are essentially exploitive, occupying all sites within the biotic and abiotic tolerance ranges of their constituent species. An increase in the absolute input of Montane Conifer pollen must result in a decrease in the percentage of Bottomland/Slope pollen, based on the nature of relative pollen diagrams, but this interaction simply mirrors real changes in the source vegetation.

An increase in the absolute influx of the Montane Conifer assemblage must be the result of an increase in the area of the source vegetation, or an increase in relative population, or increasing proximity to the basin. Such an increase in pollen must be at the expense of reduced distribution or a relatively reduced population for some other components of the forest. Because Swamp and Xeric Paleocommunities produce pollen at relatively low levels, and pine is only background "noise" in most samples, it follows that the forest unit that must have been displaced was some component of the Bottomland/Slope assemblage. Similar arguments hold for decreases in the absolute input of the Montane Conifer assemblage or increases or decreases in the absolute pollen input from the Bottomland/Slope Paleoassociation. Relative pollen diagrams certainly have pitfalls that must be avoided, but when interactions involve highly damped co-dominants in an assemblage, one can be confident that the relative frequency data are reflecting real changes in vegetation distribution.

The most obvious causal agent for such oscillation is climate, e.g., cooler conditions favoring the Montane element at the expense of the Bottomland element with the converse true in the case of a warming trend. The crucial questions then become: what was the magnitude of the thermal oscillation and over what time period did it operate?

Time Factors

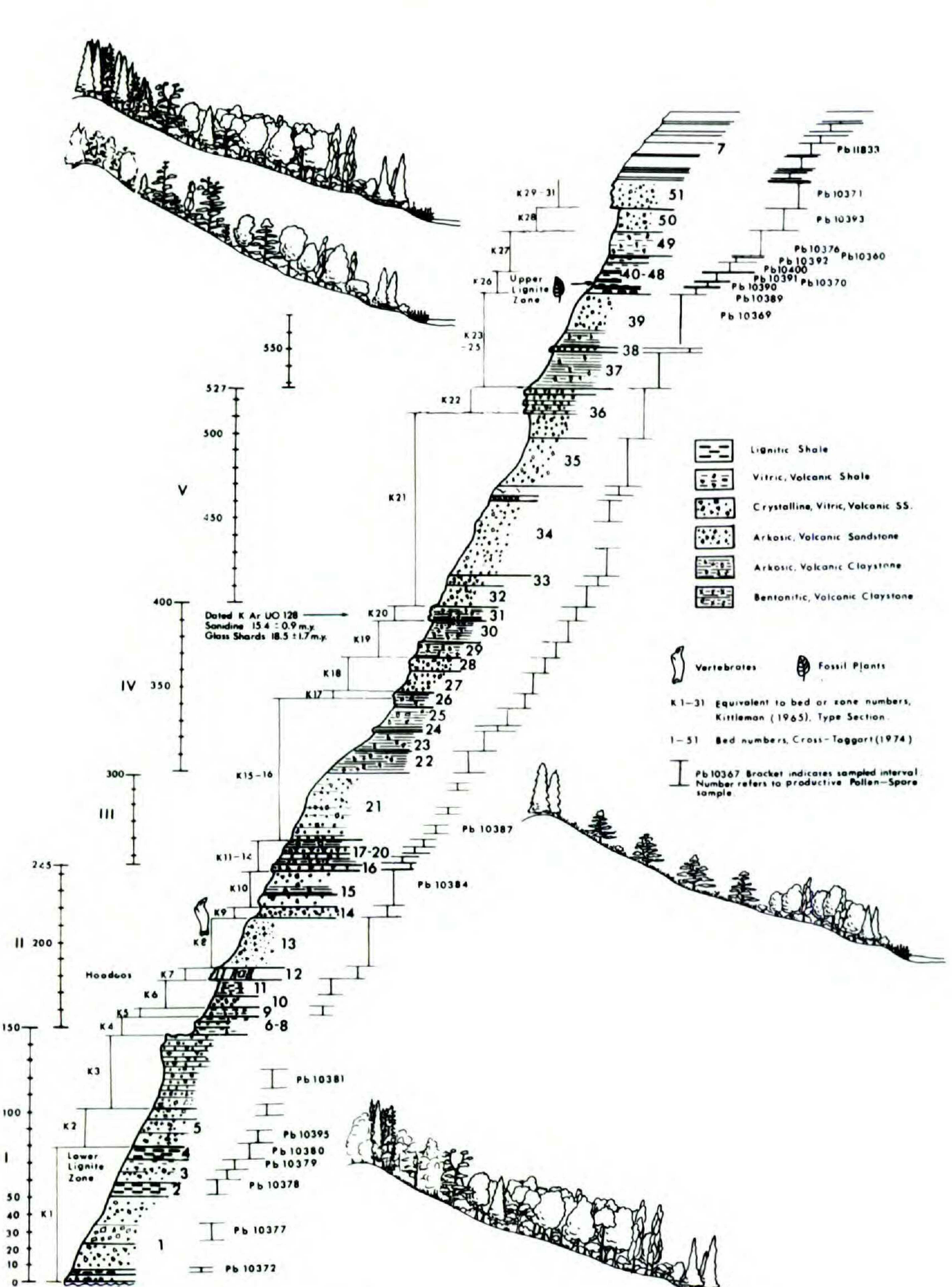
Generally the time period represented by a specific section must be deduced, since direct dating techniques lack adequate resolution. Two approaches suggest themselves: estimates based on relative sedimentary rates and estimates based on biological phenomena within the sequence in question. Although both procedures lack both precision and accuracy, there is evidence that they both converge on time spans in the order of magnitude of thousands to tens of thousands of years for most sections studied in the Miocene of the Succor Creek area. Transport and sedimentation of volcanic detritus is episodic and rates are clearly influenced by the magnitude of the eruptions and the distance and orientation of the basin from the outpouring of material relative to available modes of transport (gravity, ejection force, wind, and water). Unless a basin is quite close to the volcanic source or directly downwind, direct ash fall may be a relatively minor source of sediment. However, reworking of great quantities of ash by water transport from an extensive watershed will concentrate great quantities of ash in fluvial valleys and lacustrine basins. Unfortunately, little information is apparently available on the rates of sedimentation under such conditions.

Much more data are available for more conventional detrital sedimentation (Schindel, 1980; Spicer, 1981) although the applicability of such data may be limited for many of the Tertiary floras of the Pacific Northwest. Schindel (1980) discussed sedimentary rates extensively in an attempt to demonstrate that many biological phenomena, particularly in the context of community ecology, occur at time scales below the limits of resolution attainable by common paleoecological sampling procedures. An uncritical analysis of Schindel's conclusions might indicate that it is pointless to search for small-scale community phenomena in the fossil record of terrestrial systems. While it is not our intention to speculate as to the validity of Schindel's conclusions relative to marine studies, the success of Quaternary pollen analysis in documenting postglacial vegetation dynamics represents a *prima facie* case that the conclusions are not valid for all terrestrial systems.

If the study sections in the Succor Creek area represent very long periods of time (10^5 to 10^6 years), it follows that limited numbers of productive pollen samples are inadequate to yield useful resolution in documenting patterns of vegetation dynamics. In contrast, should the time scale represented by the sections be roughly comparable to those encountered in postglacial pollen analysis (thousands to a few tens of thousands of years), pollen analytical techniques should prove as productive in those Tertiary deposits as they have in postglacial studies. We propose that the latter situation pertains to the sections we have studied of the Succor Creek, and that the question is critical enough to present here sedimentary evidence in support of our position. The analysis has three components: the relative time periods represented by rocks accumulated under different sedimentary environments, the reasonable range of absolute time values applicable for the study sections, and the relative and absolute resolution attainable, given the productive pollen samples available.

Relative Time Equivalents of Various Rock Types.—Inland continental deposits usually exemplify two primary depositional environments, fluvial deposition in streams and rivers and lacustrine deposition in ponds and lakes. Although deposition of normal detrital sediments can be assumed to have occurred in the Succor Creek area, the bulk of the clastic material making up the Sucker Creek Formation is derived from variously altered, size-sorted, water-transported volcanic ash. Although direct ash-falls can be noted in most sections, most of the detrital pyroclastics have largely been reworked following ash falls on the Succor Creek watershed(s) with concentration of sediment in the depositional basins. Fluvial sedimentation appears to dominate through the formation as a whole (Kittleman et al., 1965), and this is certainly the case in our individual study sections. Some gravel conglomerates are known, but most fluvial deposits consist of coarse to fine-grained arkosic sands and silts. Lacustrine sediments are typically more limited in exposure and occurrence and range from relatively well-sorted shales and siltstones, through increasingly organic mudstones and siltstones, to impure lignites. The coarse-grained fluvial sediments generally accumulate more quickly than the fine-grained sediments of lacustrine systems so that a given thickness of fluvial sediment represents a shorter period of time than does an equivalent thickness of lacustrine deposit. Although both fluvial and lacustrine sediments typically have differential sedimentary rates within their own category, usually correlated with grain size, it is instructive to compare the generalized sedimentary rates for fluvial systems with those of lacustrine environments, in order to compare the relative time spans represented by the two major depositional environments in each study section.

Schindel (1980) compiled measured or inferred sedimentary rates for 15 fluvial and 29 lacustrine environments. The fluvial systems had a mean rate of 86,000 Bubnoff units per year (1 B equals 1×10^{-6} m/year) while lacustrine rates averaged 5,800 B/year. The ratio of mean fluvial to mean lacustrine rates is 14.83, implying that the average fluvial deposition rate is approximately 15 times faster then the mean for lacustrine environments. Although no exact value for relative sedimentary rates can be given, it is instructive to apply the ratio of these means, based on Schindel's compilation, to both the Whiskey Creek (Fig. 4) and Type sections (Figs. 8, 10). The Whiskey Creek section consists of approximately 102 m of sediment with the basal 53 m (52%) representing largely fluvial sands and the upper 49 m (48%) comprised of lacustrine deposits. The Type section represents 208 m of sediment, excluding the 11 m Rocky Ford sequence, of which approximately 170 m is fluvial (83%) and only 34 m (17%) is lacustrine. If we arbitrarily expand the lacustrine units by a factor of 15, followed by a uniform reduction of the entire sequence to produce a display scaled to the original section diagram, we obtain the time-corrected sedimentary plots included in Figs. 4–8. Although lacustrine sediments comprise only 48% of the measured Whiskey Creek section, they account for over 91% of the depositional time interval, assuming the 15-fold correction factor for differential sedimentary rate and no significant diastems in the sequence. Similarly, lacustrine sediments in the Type section represent only 17% of the section yet comprise 75% of the depositional time interval. Obviously such figures will shift with the differential rate factor, but lacustrine units will always represent a more significant portion of the entire



TYPE SECTION

FIGURE 10. Sedimentary sequence for the Type section showing the rock units as recognized by Kittleman et al. (1965), on the left side of the diagram (K1–K31), and the intervals we recognized when remeasuring the section during the 1974 field season, indicated by the numbers immediately to the right of the section display. A sequence of units above Unit 51 was measured and sampled in 1977. The scale on the far left side of the diagram records the cumulative thickness of the section in feet. The bracketed areas on the right side of the display indicate the position and thickness of units sampled for palynological analysis. The Pb numbers indicate the position of productive pollen and spore samples that are included in Figure 8. Our Unit 13 (K8 of Kittleman) contains vertebrate fossil material while the shale sequence represented by Units 40–48 (K26 of Kittleman) is an excellent plant macrofossil zone. Generalized vegetation reconstructions are included that show the sequence of inferred vegetation development through Type section time based on the pollen data in Figure 8. Note that the pre-disturbance vegetation at the base of the section differs from the typical "climax" forest for the region due to the relative absence of the Montane Conifer Paleoassociation, probably caused by slightly warmer temperatures in early Type section time.

sedimentary time interval than their thickness, relative to fluvial sediments, would imply.

Sampling Resolution.—This relationship of relative time interval impacts the time resolution provided by productive pollen and spore samples as well as the representation of leaves and other macrofossils. All lithologicaly identifiable sedimentary units in a section are sampled at least once and often several times. A total of only 13 of 70 samples from the Type section yielded sufficiently good recovery of fossil pollen and spores to justify quantitative analysis. The recovery rate of palynomorphs from coarse sediments, such as arkosic sands, is usually quite low. This is probably related to several factors, including increased opportunity for oxidation in coarse sediments and dilution of the pollen content due to rate of accumulation of sediment during seasonal periods when pollen levels are low. Post-depositional destruction of pollen and spores may also be a factor, a matter discussed under "Sedimentation and Alteration of Succor Creek Rocks."

The pollen recovery pattern for the Type section indicates a clustering of productive samples in the lacustrine sediments at the base and top of the section. Without consideration of the impact of differential sedimentation rates for fluvial and lacustrine sediments it would appear that a great stretch of time in the center of the section is undocumented. In point of fact, the generally satisfactory yield of samples from lacustrine sediments is sufficient to document most of the time interval represented by the section.

Absolute Depositional Intervals.—Conventional radiometric dating cannot be expected to yield data on the time interval represented by sections. Error values for single dates typically exceed 100,000 years and correspondence between dates is even less precise. Kittleman (pers. comm., 8 May 1974; 9 March 1978) cited two dates from coexisting glass shards and sanidine from a single sample from the Type section that differ by approximately three million years. While much of the differential is probably due to rapid gas migration from the sanidine, this underscores the limitations of radiometric techniques in attempting to resolve relatively short time spans in older rocks. Some varved lacustrine sediments are found in the Sucker Creek Formation but their occurrence and extent within the four study sections is too limited to provide direct sedimentary calibration.

It is instructive to apply the previously calculated mean value for fluvial and lacustrine systems to the study sections. The fluvial value of 86,000 B/yr translates to approximately 12 years for the accumulation of a meter of sediment (0.086 m/yr) while the 5,800 B/yr lacustrine value represents approximately 172 years for a meter of sediment (.0058 m/yr). In the Whiskey Creek section the 53 m basal fluvial unit would thus represent 636 years of accumulation and the upper 49 m lacustrine unit would represent 8,429 years for a total depositional period of 9,064 or slightly less than 10,000 years. In the case of the Type section, 170 m of fluvial deposits would represent 2,040 years while the 34 m of lacustrine deposits would represent 5,848 years for a total interval of 7,888 years. In this type of calculation, a major consideration, not fully taken into account in Schindel's (1980) values for rate of accumulation of sediments in different environments, is the number and magnitude of gaps in the record. We recognize the possibility, even probability, that some diastems and possibly some unconformities (where an unknown increment of previously sedimented deposits may have been removed) may exist in our sections. Recently, Sadler (1981, p. 583) noted this potential weakness in

Schindel's "constancy of sedimentation" factor, but did allow that in thinner stratigraphic sequences the determination of rates of sedimentation, where no erosion intervals are evident, probably is useful. In the sections of the Sucker Creek Formation, the continuity of the apparent paleosuccessional communities and lake beds provide some evidence that we are considering stratigraphic accumulations with only minor diastems and unconformities.

Rates of accumulation used in the previous examples are conservative when compared with the estimate of Dorf (1960), determined through a different line of reasoning, of 5.5 yr/m (.183 m/yr) for the deposition of the 365 m of pyroclastic sediments in the "fossil forest" section of Amethyst Mountain in Yellowstone National Park. McLeroy and Anderson (1966) concluded that the 15 m of lacustrine sediments accumulated in Oligocene Lake Florissant (Colorado) represented a period of 2,500–5,000 years. This estimate was based on the proportions of various types of varved laminae representing diatomite-sapropel (1 mm/yr), graded beds (8 mm/yr), and pumice laminae (1.5 cm/yr). The lacustrine sediments of our sections are comprised of rocks primarily of the graded and pumice laminae type. Assuming that the two types were equally represented, McLeroy and Anderson's values would result in a rate of 1.2 cm/yr or 90 yr/m. This rate is almost twice that of the 172 yr/m used in the examples above.

The function of this exercise is to provide a range of possible values to evaluate, in the light of other criteria, not to precisely calibrate the sections, for there are far too many variables to make that possible. Two significant points emerge. First, the absolute thickness of any section relative to the other is not a reliable guide to estimate the time that each section represents. The Whiskey Creek section, with 49 meters of lacustrine sediments, probably represents more time than the Type section, which, although twice as thick, has only 34 meters of lacustrine sediments. Second, and perhaps more important, the time periods indicated for such rock units are in the order of thousands to tens of thousands of years. If sedimentation was an order of magnitude faster we would be dealing in only centuries, while we might have to consider as much as 100,000 years, if sedimentary rates were an order of magnitude slower. Extremely slow sedimentation seems unlikely since availability of relatively unconsolidated ash could be expected to result in very rapid accumulations of thick bodies of water-transported ash sediments in the topographic lows. Although ash availability was episodic, it was probably superabundant when available, as witness the rapid ash blockage of the Toutle River in Washington with the eruption of Mt. St. Helens (Rosenfeld, 1980, p. 504).

The paleobiological data from the pollen spectra seem generally in accord with the order of magnitude implied by this rough attempt at calibration. The basal fluvial sand at the Whiskey Creek section represents 636 years at the 86,000 B/year rate and this value may be conservative. A clay shale immediately below the fluvial unit, a calcareous ironstone approximately half-way up the unit, and a shale overlying the sand, all yielded essentially similar pollen spectra. It is probable that the source vegetation was essentially the same in each of the three cases, implying that little time elapsed during the accumulation of the basal sand. Similarly, the swamp interval documented in the upper Whiskey Creek section would have required between 2,000 and 4,000 years based on the calculated value of approximately 8,400 years for the lacustrine unit. Such a value is not unreasonable for hydrologic succession in a modest-sized lake and, if in error, is perhaps on the long side.

In summary, the exposed stratigraphic sections in the Succor Creek area appear to represent geologically short time intervals (several thousand to several tens of thousands of years) within the one to two million year span of Sucker Creek time. Although much of Sucker Creek interval is probably undocumented by continuous sedimentation, each study section represents a time period wherein we might expect to discern vegetation dynamics in forest communities.

Climax Vegetation Dynamics

The fluctuations in the relative importance of the Montane Conifer and Bottomland/Slope Paleoassociations probably occur over intervals ranging from several centuries to a few thousand years. If this is the case, it would argue for relatively small temperature fluctuations. The mosaic of Succor Creek forest communities may well have represented a relatively delicate distributional equilibrium in response to the then-current mean annual temperature and annual range of temperature. Slight shifts in either parameter over a period of centuries would result in a redistribution of the community mosaic. No evidence exists for extreme topographic relief in the area during Sucker Creek time and if we assume the vegetation to have been developed on low-slope gradients, such gradients would amplify the effect of slight elevational shifts in ecotones, greatly increasing the area of one forest type relative to the other and greatly increasing or decreasing the distance that pollen might have to be transported. Small thermal oscillations thus appear sufficient to account for the observed shifts in the relative importance of the Bottomland/Slope and Montane Conifer Paleoassociations. These thermal oscillations will be discussed later in the context of cliseral succession.

POST-DISTURBANCE SUCCESSION

Volcanic Disturbance

The most dramatic feature of the pollen profiles of the Rockville, Shortcut, and Type sections is an abrupt change in the composition of the pollen flora at some stratigraphic level in each of the sections sampled. In each section the transition is marked by a significant decrease in the frequency and diversity of the Bottomland/Slope Paleoassociations with an increase in the importance of the Xeric Paleoassociation and a complex of "Other" pollen representing angiospermous plants of unknown taxonomic affinities. The Montane Conifer Paleoassociation is an important element in the lower Rockville and Shortcut sections. At the transition point in these two sections, the pollen of the Montane Conifer complex declines to insignificance, concomitant with the decline of the Bottomland/Slope element. It is not represented at the base of the Type section but is represented in significant amounts in the nearby Rocky Ford section which is of uncertain stratigraphic position

We described this phenomenon and suggested that the shift of dominance from one type of vegetation to another, as shown in pollen diagrams (Taggart & Cross, 1974, figs. 2 and 3), might be related to a secondary succession initiated by volcanic disturbance of the forest vegetation or a cliseral succession due to a pivotal change in regional climate. With the accumulation of additional data from the Type section, where the pollen diagram indicates the eventual return of diverse forest vegetation, the succession hypothesis was greatly strengthened. We have discussed this concept in detail in a recent paper (Taggart & Cross, 1980). On a time scale measured in thousands of years, the forest habitat in the Succor Creek area was clearly unstable. It was subjected intermittently to various types of volcanic catastrophes: direct ash falls of considerable thickness, ash flows of high temperature and velocity, blast effects of violent explosions, the poisonous effects associated with gas venting, mudslides that commonly accompany major volcanic activity near the source, and damming by flows and sediment choking of valleys causing extensive muddy lakes. Tertiary paleobotanists have considered the mechanical effect of ash falls and the lethal effects of gas venting in facilitating leaf fall, but most, with exceptions such as Dorf, in his studies of the Eocene "fossil forests" of Yellowstone National Park (1960, 1964) and Axelrod (1968, p. 720), have not considered the impact of regional volcanism on forest vegetation dynamics. The Yellowstone sequence clearly indicates that ash falls, mud flows (lahars), and fluvially transported ash accumulations periodically buried existing forests, and these, acting together with accompanying noxious gases and occasional explosive forces, probably destroyed all vegetation especially at the sites of the deposition of thicker ash layers. We have suggested that the abrupt decline in the number and diversity of Bottomland/Slope elements in the Rockville, Shortcut, and Type sections and a concomitant decline in the Montane Conifer element at Rockville and Shortcut, represent incidents of intermittent destruction of extensive areas of the forest vegetation in the Miocene of the Succor Creek region. The magnitude of areas stripped of vegetation would have varied with the duration and size of the volcanic outbursts.

When extensive disruption of Succor Creek vegetation by volcanic activity was first proposed as a hypothesis to explain the sudden transitions in the Rockville, Shortcut and Type section pollen diagrams (Taggart, 1971; Taggart & Cross, 1974, 1980) such a reconstruction might well have been considered extreme. But the explosive eruption of Mt. St. Helens on 18 May 1980 provides a graphic example of the effect of local volcanic activity on diverse forest vegetation. Rosenfeld (1980) gives a wealth of interesting observations regarding the effect of this eruption on surrounding communities. He noted that near the breached north side of the mountain (in background of Fig. 12) nearly every slope exposed to the blast within 10 km was denuded of vegetation and covered with ash and to 15 km, trees were stripped of their branches and snapped off at their bases. Trees

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FIGURES 11–12.—11. A ridge north of the Toutle valley showing the directional effects of the blast accompanying the 18 May 1980 eruption of Mt. St. Helens in southwestern Washington. The right side of the ridge in this photo, facing the blast, was scoured of vegetation and blanketed with ash. The forest on the lee (left) side of the ridge suffered less disruption with singeing and burning of leaves, stripping of branches, and felling of some trees. (This photo, provided by Charles L. Rosenfeld, was originally published in Rosenfeld, 1980, Amer. Sci. 68: 500.)—12. The northwest shore of Spirit Lake, with Mt. St. Helens in the background, following the 18 May 1980 eruption. The blast, 11

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projected directly from the volcano some 10 km distant, hurled blocks of rock over 20 m in diameter into this area. Blast forces and the downward thrust of mud and other debris into the far side of the lake pushed a wall of lake water northward, scouring slopes up to 300 m above the original lake level. The mud and log-strewn landscape in the foreground represents the aftermath of this surge. (This photograph, provided by Charles L. Rosenfeld, was originally published in Rosenfeld, 1980, Amer. Sci. 68: 501.)

on lee slopes were left standing but their leaves were singed or burned (Fig. 11). The force of the blast and displacement of debris forced the waters of Spirit Lake 300 m up the slope of Mt. Margaret, effectively denuding that area of vegetation cover (Fig. 12). Landslides and debris-flow scoured hillsides, removing more than a meter of soil in many areas. Ancillary effects of the blast include the creation of impounded lakes in tributary valleys unaffected by the primary blast, the possibility of high sediment yields and additional mudflows with the re-establishment of drainage channels, and the extreme erosional instability of slopes denuded of vegetation cover. In lowland areas, the ash, compacting underlying organic debris, has created a mosaic of depressions that are already acting as small depositional basins. As impressive as the eruption of Mt. St. Helens was, it is insignificant relative to the magnitude of the events leading to the massive pyroclastic Tertiary plateaus of the Pacific Northwest. In referring to such deposits, Heiken (1979) suggested, ". . . Such eruptions would be awesome, burying hundreds of thousands of km^2 under pyroclastic flows that move away from the vent at hurricane velocities. Eruption clouds may deposit fallout over millions of km^2. A safe distance from which to watch such an event might be the earth orbit of a space station . . . ."

While our interpretation of the Rockville, Shortcut, and Type sections assumes catastrophic destruction of forest vegetation, we may in fact be understating the magnitude of disturbance. Where sufficient ash exists to preserve a flora or fauna, it is quite reasonable to expect a discontinuity or change in the plant or animal record signifying a community disruption.

The events following widespread destruction or disruption of a forest community depend on the areal extent and magnitude of the damage, and the biotic potential of the region. In an extant biota, many species exist that are adapted to colonizing or pioneering strategies. Such species will exploit open, often drier, habitats, sometimes leading to the establishment of a secondary succession in which the post-disturbance area is initially dominated by forbs and grasses. Under a mesic climatic regime trees and shrubs will seed into the area, either from seed pools in the soil or by dispersal from relict areas or undisturbed peripheral communities. Thus a period of forb dominance is usually succeeded by a shrub stage, followed, barring further disturbance, by the gradual re-establishment of a forest system. Such a succession requires a considerable range of ecological diversity in the regional flora, including the pioneer species characterizing the early seral stages.

The Eocene Yellowstone biota may well have lacked the diversity for a distinctive early successional sequence. Megafossil studies by Dorf (1960, 1964) and pollen analysis by Fisk (1976) indicate that recovery consisted of the recolonization of the area by essentially the same species that constituted the pre-disturbance forest. This is not surprising because herbaceous dicots, grasses, and even many shrubs apparently are poorly represented in the Eocene (Leopold, 1969, p. 382). It is these groups of plants that characterize the earlier stages of the distinctive successions that can be documented for extant floras.

By mid-Miocene time, however, such plants had undergone considerable evolution. In the Succor Creek, herbaceous dicots (Chenopodiaceae, Amaranthaceae, Compositae, Malvaceae, Onagraceae), grasses (Gramineae), and woody shrubs, are well-represented (Graham, 1965; Taggart, 1971, 1973; Taggart & Cross 1980). The pollen record appears to indicate a role for such plants in distinctive post-disturbance succession. A recently ash-covered landscape is inherently edaphically dry (Bowman, 1911, pp. 203–205; Leopold & MacGinitie, 1972, p. 174) and, even in areas of abundant rainfall, such a surface generally does not represent a suitable seed-bed for the re-establishment of forest trees. Such habitats are within the adaptive range of exploitation by numerous herbaceous species. The peaks in the pollen profiles representing the Xeric Paleoassociation (principally Compositae, Gramineae, Chenopodiaceae/Amaranthaceae, and Malvaceae), which appear following the disturbance transitions at the Rockville, Shortcut, and Type localities, indicate initial colonization of the ash-covered landscape by these taxa (Fig. 9-I). Although a variety of shrub and tree species may have begun seeding into the area during the post-disturbance herbaceous stage, the most consistent feature, best documented at Rockville, is a rise in the level of pine pollen, indicating the development of a pine-stage later in the successional sequence. Pine pollen is at about 10% in the samples of sediment deposited immediately before or shortly after the disturbance, which is essentially the level of pine in the regional "background." However, the relative frequency of pine rises to 69% at the top of the Rockville section. Post-disturbance levels of pine reach about 30% in the Shortcut locality and 45% in the Type section. Although such levels are not sufficiently high to suggest a closed-canopy pine forest (Leopold, 1964), they do suggest an open, second-growth pine assemblage that may have provided shelter for establishment of seedlings of more shade-tolerant forest species (Fig. 9-II). Whereas the Rockville record ends with this "pine stage," the Type section record continues on to later stages and indicates that sweetgum (*Liquidambar*) and hickory (*Carya*) may have been significant components in the post-pine reforestation continuum (Fig. 9-III).

Although the immediate post-disturbance pollen record for the Bottomland/Slope element is low in diversity and in importance, it does persist. The pollen record indicates a limited riparian assemblage consisting of relict forest remnants or species that were able to become re-established relatively rapidly on the more mesic sites near lakes and streams. The Bottomland/Slope community diversity averages 19 taxa per sample, while the two post-disturbance samples average only 6 taxa. Oak, willow, and sycamore are the most prominent components of this riparian thicket.

The uppermost series of samples from the Type section record the return of forest vegetation, including both the Bottomland/Slope and Montane Conifer elements with diversity ranges comparable to the forest records throughout the study area (Fig. 9-IV). It is possible however that the Bottomland/Slope forest component of the upper Type section may be sub-climax in nature since it is dominated by oak in contrast to the elm dominance characteristic of the Whiskey Creek, lower Rockville and Shortcut, and lower Type sections. The megafossil record for this forest includes *Ulmus, Zelkova, Populus, Salix,* and *Carya.*

Objections to the Succession Hypothesis

Paleobotanists have documented cliseral succession in the Tertiary of the Pacific Northwest, both regionally (Chaney & Axelrod, 1959) and locally (Shah, 1968; Smiley et al., 1975b), but our Succor Creek Flora studies may represent one of the first attempts to document post-disturbance succession (primary or secondary) in a Tertiary flora. It is reasonable to ask why such processes have not been identified previously, or if alternative explanations might provide a better interpretation of the data we have presented. We will briefly discuss some issues that may bear on these questions.

Limited Resolution.—The research of Schindel, 1980, would suggest that the recognition of processes such as succession is beyond the range of resolution in conventional paleobiological studies due to the duration of the process relative to the rate of sedimentation. In point of fact, Quaternary pollen analysis of bogs and lakes has proven successful in documenting both secondary and cliseral succession using sampling of variable intensity. The accumulation of lake muds and peat is a slow process with a high constancy factor, in the terms of Schindel (1980). The remarkable Clarkia Lake Beds, now under intensive study by Dr. Jack Smiley, University of Idaho, and others (Smiley et al., 1975a; Smiley & Rember, 1979, 1981; Rember & Smiley, 1979; Niklas & Brown, 1981; Giannasi & Niklas, 1981; Smiley & Huggins, 1981; Lewis, in press), is a Miocene deposit (est. age 20 m.y.) of slightly more than eight meter thickness of thinly-laminated lake beds containing remarkably preserved leaves, fruits, seeds, flowers, pollen and spores, algae, and several types of fauna. This is a prime example of a fossil flora showing continuous changes in plant community structure in an identifiable unit of time, possibly several centuries. Another example of fine stratigraphic and temporal resolution possible, is the landmark study of Zangerl and Richardson (1963) on the Mecca Quarry Shale Member of the Linton Formation (Pennsylvanian) of Indiana. There, the resolution of the biotic changes and sediment deposition were recorded and amply documented as a year-by-year series of events for a depositional period of less than five years. This finely-laminated black shale was nearshore black mud deposited in very shallow water of a transgressing sea. Detailed stratigraphic palynology of a flora, such as the Succor Creek, is merely the logical extension of the use of a proven analytical tool.

In the Whiskey Creek lignite beds, sampling was made at intervals comparable to those employed for Quaternary pollen analysis, but the results obtained indicate no new patterns of interaction. The Upper Lignite Series diagram (Fig. 5) indicates a pattern of mutual oscillation between Montane Conifer and Bottomland/Slope elements, similar to that seen in the main section (Fig. 4). The pattern of increasing Swamp pollen levels in the Upper Lignite Series is consistent with the trend in the section as a whole and there is generally a satisfactory "fit" between the pollen levels in the uppermost samples from the Upper Lignite Series and the overlying shales, as documented in the main Whiskey Creek pollen diagram. The fit between the main section diagram and the lowermost Upper Lignite samples is quite poor however and may indicate the effects of limited resolution in the main section diagram. The transition back to high levels of Montane Conifers, as indicated in the basal samples from the Upper Lignite Series, occurs in approximately 1.5 meters of strata and is comparatively abrupt when compared with most such shifts noted in either the main Whiskey Creek section (Fig. 4) or the Upper Lignite Series diagram (Fig. 5). It is possible that the shale-lignite transition represents a diastem of unknown duration or the abrupt change in pollen levels may signify a relatively rapid return of well-developed conifer forest in the area. The 1.5 meters of intervening section would represent a period of approximately 300 years using the criteria previously discussed so it is possible that the transition may mark a shift of community types requiring only a few centuries for completion. Detailed sampling through the shale unit and into the Upper Lignite Series would be required to resolve the question.

Whether fortuitously or by some design, virtually all of the successional events in our sections occur in coarse sediments with higher rates of sedimentation, which may indicate diastems or times of rejuvenation of erosion cycle. Even the limited productivity of such samples is sufficient to identify the presence of the process.

Lack of Previous Recognition.—Recognition of the occurrence of a post-disturbance succession at several sites in the Succor Creek area is possible only because we have undertaken detailed pollen analysis with very close stratigraphic control. Palynology is an ideal tool for documenting some types of events that occurred during the time-frame represented by sediments, even though those events may have occurred at sites or in regions at some distance from the basin of deposition. This is particularly true for herbaceous plants, which are usually poorly constructed for efficient representation. Quaternary pollen analysis is conducted with high sample density to record such phenomena and they can be and are distinguished. Most conventional stratigraphic palynology studies of Tertiary rocks are conducted to establish regional correlations of larger stratigraphic units (formations, members, etc.) and thus lack the resolution necessary to recognize temporally restricted phenomena such as secondary succession. Conventional Tertiary paleobotany in the Pacific Northwest primarily has involved evaluation of macrofossils and most of the classic studies lack detailed stratigraphic control. Axelrod (1968, p. 720, footnote 2) states that paleosuccessional stages following destruction of forests by ash-falls or fire have been identified in association with four fossil floras; two Eocene, Bull Run (Nevada) and Germer Basin (Idaho), and two Miocene, Carson Pass (California) and Purple Mountain (Nevada).

The most likely recognition feature for a successional community in the macrofossil record would be a low diversity florule. Taggart and Cross (1980) have indicated that low diversity florules in the Succor Creek (dominated by willow, oak, and sycamore) correlate closely with the successional intervals indicated in the pollen stratigraphy. One must have adequate stratigraphic information to rank florules as to time of occurrence and it is unlikely that the significance of even the low-diversity Succor Creek florules would have been appreciated without the framework provided by detailed stratigraphic correlations and concurrent pollen studies.

Finally, no matter how detailed the information available for a time sequence, disturbance that initiates succession must occur within the period of time represented by the sedimentary sequence studied. If a catastrophic disturbance does not occur, one may be able to document hydrologic succession or even cliseral phenomena, but primary or secondary succession, on a recognizable scale, would be missed. The profile for the Whiskey Creek section, documenting perhaps ten thousand years of forest history, is a case in point. Presumably massive disturbance in the Whiskey Creek area did not occur during the period represented by the section exposed and studied. Although the pollen profile of the Whiskey Creek section, and the excellent macroflora preserved at several levels, provide an interesting record of hydrologic succession and climax vegetation dynamics, post-disturbance succession was not recognized.

Cliseral Model.—The final possibility to be discussed involves the consideration that, because of poor or insufficiently detailed temporal resolution, we are not looking at succession at all, but rather are dealing with long-term cliseral shifts in vegetation dominance. The data from the Type section indicate that the transition from mesic forest to vegetation of xeric aspect is not irreversible; the forest, in fact, returns eventually in that section. If the study sections represented time intervals on the order of millions of years they would then record pronounced climatic oscillations (mesic to xeric to mesic) on a scale never before suggested and the absence of a similar record from the Whiskey Creek section would be enigmatic. There is no evidence for evolution of Succor Creek taxa in the microfossil and macrofossil records, which is further evidence that a relatively short time is represented. Climatic oscillations in the short term, exceeding those of the Pleistocene, seem unlikely. The post-disturbance record is not a random sampling of xeric vegetation; rather, a directed sequence is discernible, consistent with known trends of secondary succession.

It might be argued that what is reflected are simply the equivalents of facies changes, indicative of depositional sites in an active fluvial or deltaic system with bars, levees, crevasse splays, or other features simply supporting different localized vegetation types. This might well be the case for a series of leaf floras, given the localized nature of leaf deposition, but this is unlikely when relative continuity of the pollen record is considered. During Whiskey Creek time, the sedimentary record indicates a high level of fluvial and lacustrine activity, yet no parallel phenomena of floral response to those local physiographic or edaphic changes can be noted, probably because the pollen record reflects the broader regional vegetation array. Succession, initiated by local volcanic activity seems to be the most uniformitarian and rational model for the data available.

Fire Initiated Succession

Although the major transitions in the Succor Creek pollen record have been attributed to volcanic disturbance over a wide area, fire as an initiator of localized succession is to be expected, particularly in areas supporting extensive conifer forests. In recent years increasing attention has been paid to the role of fire in regional vegetation dynamics (Bormann & Likens, 1979; Habeck & Mutch, 1973; Wright & Heinselman, 1973; Loope & Gruell, 1973; Swain, 1973; Rowe & Scotter, 1973). Fire is apparently a more frequent disturbance factor in coniferous forests and Rowe and Scotter (1973) note that fire incidence in mixed broad-leaved/coniferous stands increases with the proportion of evergreen trees in a stand. Daubenmire and Daubenmire (1968), referring to the forests of the northern Rocky Mountains, considered the probability of fire incidence to approach unity in a period of 450–500 years on a specific site. Hemstrom and Franklin (1982) reported a 465 year interval for natural fire rotation in the coniferous forests of Mt. Rainier (Washington). The most probable ignition source for such fires is lightning. Loope and Gruell (1973) stated that nowhere in the world is lightning a more significant source of ignition than in the coniferous forests of the Pacific Northwest, citing rates of between 53 and 60% for lightning induced fires in this region. Rowe and Scotter (1973) noted that during one seven year period, 27% of all forest fires in Canada were lightning induced. Habeck and Mutch 1973, p. 410) stated that a high percentage of vegetation in all forest zones has been disrupted by fire and is at different stages of recovery. Forest stands that have reached climax or near-climax are only rarely found, and these only because those stands have fortuitously escaped fire for several centuries. He noted that past, uncontrolled fires did not usually create a completely burned over, denuded area at any one point in time as is evidenced by the many stages of development found in each forest zone.

Although fire may have been a disruptive influence on any of the forest types of the Miocene of the Succor Creek region, the Montane Conifer forests were probably most susceptible. Fire disturbance would most likely be reflected in a sudden decrease in Montane Conifer pollen levels, reflecting the loss of the source forest-cover type, followed by a recovery period. Loope and Gruell (1973) noted a pattern of initial pine dominance in burn areas in Wyoming, followed by a transition to spruce dominated forests with a gradual increase in the importance of fir. Such interactions might well be a factor in Miocene burns as well. In a well-watered area, disruption by fire would almost certainly be more limited than the widespread effects of ash falls and other secondary effects of volcanic activity and recovery might be reasonably rapid, with reseeding from surrounding areas not damaged by fire (Hemstrom & Franklin, 1982, p. 47).

One case that might represent a fire-initiated succession in the Succor Creek pollen record can be noted during the Montane Conifer/Bottomland Slope forest interval at the base of the Rockville section (Fig. 6). Here spruce pollen levels peak at over 50%, dropping to 10% in the next sample up the section ($\simeq$1.5 m). This sample also contains a large number of very small charcoal (fusian) fragments. Subsequent samples record a recovery in Montane Conifer pollen levels prior to the critical transition zone in the section. It is interesting to note that this abrupt Montane Conifer decline in the basal Rockville sediments occurs at a point where Pine starts a modest increase. This point is also marked by a small peak in Xeric pollen types. This very sharp oscillation in Montane Conifer levels might well represent a local burn, causing an abrupt decrease in the contribution of Montane Conifer taxa to the pollen record. Furthermore, the Xeric pollen peak may represent an influx of herbaceous plants into the burn area, followed by Pine and Montane Conifer elements. Over a period of several centuries one would expect Pine levels to drop as the Montane Conifer elements re-achieved ascendency and such a pattern is consistent with the pollen profile.

Although fire may play a role in defining the interaction of Montane Conifer and Bottomland/Slope elements, most of the oscillations between these two groups are more gradual in nature, suggesting the possibility of climatic control. This subject will be discussed in the following section.

CLISERAL SUCCESSION

Although the pattern of vegetation on a specific site may be modified by a variety of edaphic, biotic, or microclimatic factors, and by action of pseudoperiodic agencies such as fire, wind, water and disease, it is a well-accepted concept in phytogeography that climate plays the dominant role in determining the nature of regional vegetation (Cain, 1944). Any significant change in the components of regional climate, mean and range of annual temperatures, annual precipitation, or shifts in rainfall distribution, can be expected to induce changes in the nature and distribution of vegetation in the region. The climatic control concept is so well-established that the nature of terrestrial vegetation as reflected in the fossil record serves as the primary means of reconstructing Late Cretaceous and Tertiary paleoclimates for continental deposits. Unfortunately even if the nature of a fossil flora is well understood, no linear conversions exist to transform a specific fossil data set into the context of world paleoclimate due to a variety of factors, including elevation, slope exposure, and the degree of thermal buffering provided by nearby seas or large inland lake systems. Tertiary paleobotanists have adopted two distinctly different approaches to resolve this dilemma and profound differences of opinion on Tertiary climatic trends have emerged.

The ecological school of paleoclimate, pioneered in the studies of Ralph W. Chaney and further refined by Axelrod (Axelrod, 1968; Axelrod & Bailey, 1969), postulates a period of gradual cooling through the Neogene with vegetation development modified regionally in the Pacific Northwest by the development of the rain shadow of the Cascades. In this model, cooling is accompanied by a decrease in equability and the only short-term changes in annual temperature that occur are the result of elevational changes related to uplift.

The foliar physiognomy approach to paleoclimatic reconstruction, led by Wolfe (Wolfe & Hopkins, 1967; Wolfe, 1978), postulates a sharp drop in mean annual temperatures in the Oligocene with relatively constant mean annual temperatures from that point to the present day. Wolfe (1978) suggested a pattern of mild late Tertiary mean annual temperature oscillations in his graphic presentation of the data (see also Dorf, 1959), but stated that altitudinal differences provided sufficient uncertainty in the Pacific Northwest record to preclude detailed conclusions. He did state however that the Miocene record is characterized by an increase in equability with drops in summer maxima counteracted by increases in winter minima.

We have stressed previously the evidence for a cool but equable climatic regime to reconcile the macrofossil and microfossil data for the Succor Creek Flora. While our data support the equability component of Wolfe's reconstruction (1978), we suggest somewhat cooler temperatures than he indicated for regional Miocene floras and the relative constancy of the thermal regime is open to some question. Definitive long-term thermal trends on the Succor Creek Flora have proved to be impossible to demonstrate with the data currently available. Shah (1968) and Smiley et al. (1975b) documented what they believed to represent a definitive cooling and drying trend throughout the middle to late Miocene based on a sequence of Miocene and Pliocene floras from the Weiser area of Idaho. The absence of Montane Conifer Paleoassociation pollen from the strata of the lower Type section record, and its presence in the upper part of the section led us (Taggart & Cross, 1980) to postulate a slight cooling trend through the time represented by the Sucker Creek Type section with early Type section temperatures being sufficiently high to exclude the Montane Conifer element from adjacent uplands. We noted that reduced elevation in the Type section area, coupled with modest topographic relief, might require only slightly higher temperatures to achieve such an exclusion. Although there is no reason to alter the assessment of the relative temperatures in early as opposed to late Type section time, new evidence from above and below the measured Type section makes it unlikely that this difference in temperature represents a definite trend.

Additional strata above the Type section have now been measured and sampled and an additional productive pollen sample located approximately 6.5 m above the top of the measured section has now been tabulated. This sample contains approximately 23.3% Montane Conifer, 55% Bottomland/Slope, 12.5% Swamp, 2.5% Pine, 2.5% Xeric, and 4.2% Other pollen. Therefore, this is comparable to the productive samples from the upper Type section already reported.

The top of the Rocky Ford section, a unit about 11 m thick, located across the Succor Creek Valley, correlates to within a few meters of the base of the measured Type section. Pollen spectra from two productive samples obtained from the unit are very similar to those from the Succor Creek sections to the south (averaging 39% Montane Conifer pollen) and indicate even cooler conditions than those in upper Type section time. Thus in the Type section area the pollen record indicates a cool interval during Rocky Ford time, followed by a warmer interval in early Type section time. By the time forest vegetation had returned following disturbance in middle Type section time, temperatures had dropped again, although late Type section time was apparently slightly warmer then during Rocky Ford time (Fig. 10). The pollen record from the Type section thus supports the same oscillatory temperature model discussed previously in terms of climax vegetation dynamics. It should be noted that although these thermal oscillations have very distinctive pollen signatures, the magnitude of the oscillations need not have been very great to have caused the observed pollen shifts if slope gradients were sufficiently low.

Marine studies of foraminifera and oxygen isotope ratios indicate definite thermal oscillations throughout the postglacial, the "Little Ice Age" being the most significant excursion of this sort in the historical record. Imbrie and Imbrie (1979) have suggested that such oscillations are the result of interactions of cycles in earth orbit mechanics (eccentricity, tilt, and precession) as proposed by Milankovitch (1930) as a theory to explain the origin of Pleistocene glaciations. Our studies indicate that considered in time, spans of thousands to tens of thousands of years, Miocene climates in the Pacific Northwest exhibited a similar oscillatory thermal regime. Given the magnitude of this oscillation and the limited time represented by the rocks of the Sucker Creek Formation, it is unlikely that the Succor Creek Flora, or any single flora for that matter, can provide definitive data on the existence of any overall trends superimposed on this pattern of thermal variability. Our data do suggest however that unless the scope of thermal variability for a fossil assemblage can be assessed, caution must be used in integrating the thermal indications of a flora into a regional model for climatic trends. This *caveat* would appear to be equally applicable to climatic modeling based on foliar physiognomy or ecological affinities.

GEOLOGIC CONSIDERATIONS

Physiography and Topography in Consideration of Regional Climate

The Columbia Plateau, Basin and Range, and Snake River Plain Provinces, which surround this Succor Creek area, are physiographic provinces established on the basis of some unifying fundamental geologic characteristics, as well as topographic features. The Succor Creek area is generally considered to be an eastward extension of the Columbia Plateau Province, but there is some evidence that it may actually be a part of the Basin and Range Province (see Fig. 3). The Owyhee Mountains seem to be isolated from the rest of the Plateau region as an island-like mass rising above the surrounding volcanic plateau.

Some attempts have been made to establish the paleoelevation of the Succor Creek region on the basis of the fossil flora. Axelrod (1964; 1966, text-fig. 12; and 1968, fig. 7B) considered the Succor Creek forests to have been developed at an elevation of less than 300 m, based on considerations of effective temperature and equability as indicated by the leaf flora. Axelrod (1966) defined the composition and altitudinal zonation of the dominant forest communities of the Miocene of the Columbia Plateau region as:

1. broad-leaved evergreen forests (below 150 m)
2. mixed deciduous hardwood forests (150–500 m)
3. montane conifer/deciduous hardwood forests (500–1,000 m)
4. montane conifer forests (above 1,000 m)

Our data indicate that the Succor Creek forests might be classified most appropriately as montane conifer/deciduous hardwood forest in the framework of Axelrod's 1966 terminology, probably near the high side of the 500–1,000 m zone. It is likely that the prevailing mean annual temperature and range of temperature was such as to permit the Succor Creek basins to support predominantly evergreen oak forests, with deciduous hardwood forests on adjacent low slopes, grading ecotonally into conifer forest of montane aspect on adjacent uplands of moderate elevation relative to the valley floors. Wolfe (1969, p. 93) argued that the Succor Creek Flora ("Rockville") was probably an upland area of at least "moderate elevation," based on geological considerations relating the Succor Creek deposits to those of the Latah, Mascall, and Fish Creek Floras. Their stratigraphic positions on or interbedded with the Columbia River Basalt indicate mid-Miocene elevations of 500–750 m. Wolfe and Hopkins (1967, p. 71) indicated that the percentage of entire-margined leaves in the Succor Creek ("Rockville") Flora is 30%, indicative of a temperate assemblage (Wolfe, 1969, p. 87). As we noted previously, there appears to be no valid reason for separation of the Succor Creek Flora into two or more temporally distinct assemblages. Taken as a whole, about 25% of the Succor Creek woody dicot leaf species have an entire margin, reinforcing the assignment of temperate aspect to the bottomland assemblage. Such an analysis, however, overlooks the variation in the composition of individual florules. Only a single Succor Creek florule, that from the Fenwick Ranch (Graham, 1965), has the requisite 30 dicot leaf taxa to justify quantitative analysis of leaf margin data within a 5% margin of error (Wolfe, 1971, p. 36). In that case, the percentage of entire margins in the dicot florule is approximately 30%. Only two other florules have in excess of 20 woody dicot leaf taxa (McKenzie Ranch and the Carter Creek localities, Graham, 1965), and these show entire-margined dicot leaf percentages of 14% and 28%, respectively. This range of variability exceeds that used by Wolfe (1969) to demonstrate that the sequence of Neogene floras in the Columbia Plateau region represents variation in thermal regime with time, as opposed to the altidudinal zonation suggested by Axelrod (1964), and encompasses a range of climate from cool temperate to warm temperate (Wolfe & Hopkins, 1967).

We are not committed to either an altitudinal or temporal change model for any combination of the Neogene floras of the region, but we consider that the data available are simply too variable to suggest unambiguous validation of either model. Both pollen and leaf-margin data suggest that the climax vegetation, supported on any specific site within the Succor Creek area, was variable, and subject to a variety of site factors. We know, on the basis of the stratigraphic studies of specific sections, that the development of specific forest types was subject to modification based on short-term climatic fluctuations and the action of disruptive events such as volcanic disturbance and fire. To the extent that similar variability can be assumed to exist in other areas within the region throughout the Neogene, generalizations simply are not justified where they are based on small numbers of pollen spectra, on isolated, individual floras, or particularly, where based on "composite" assemblages where routine taxonomic treatment tends to mask florule diversity. Such generalizations may be misleading in the context of a single flora, suggesting the need for caution in the creation of broad regional models of any sort.

We have postulated the area to have been a low-gradient upland plateau during mid-Miocene, possibly a northward or northwestward sloping paleoslope (Taggart & Cross, 1980). This upland must have had either a high enough elevation or a climate cool enough to support, at least intermittently, a montane conifer forest within a few km of the fluvial and lacustrine sedimentary basins in which the macrofossil floras accumulated. To account for this, we will evaluate some other geological features of the area that suggest a greater elevation of the region during Succor Creek time.

Principal Structural Features Relevant to Succor Creek Vegetation Development

The tectonic history of the Succor Creek area is intimately related to the Basin and Range Province to the south and west, to the Snake River Plain to the east, and to the Columbia Basalt Plateau to the north (Fig. 3). A major tectonic boundary in this area marks the western margin of the continental craton and the eastern edge of the Phanerozoic "eugeosyncline." This line has been identified as extending in a general north–south direction and passes just east of the Oregon-Idaho state line. This suture, or margin of two adjoining crustal plates, passes directly through the Owyhee Mountains (Fig. 2) and the eastern portion of the Succor Creek area (Armstrong et al., 1977, fig. 10; Davis, 1979, fig. 2). This line also crosses the Snake River Plain near its western end and may possibly be related to some structural features of that graben. Armstrong et al. (1977) and

Davis (1977, p. 4) have postulated the position of these plate margins within 10 km on the basis of the ratios of Sr^{87}/Sr^{86} in igneous rocks of the area. Later rocks are mostly of Mesozoic age in the southeastern Oregon-southwestern Idaho area. Ben-Avraham (1981) proposed that an exotic sliver or fragment (microcontinental plate) of allochthonous terrain adjoins the Precambrian North American plate on the west at this suture. Davis further suggested (1977, p. 35) that this suture is a zone of crustal weakness that was reactivated in Miocene times during the ENE–WSW regional extension. Davis (1979, p. 43) also noted that the dike swarms in eastern Oregon-western Idaho, from which most of the eastern area of the Columbia River Basalts were probably extruded, lie directly west of this north–south tectonic boundary. The southern margin of the dike-swarm area lies about 25 km north of the Succor Creek area. On the basis of gravity and magnetic anomalies, Mabey (1976, p. 55) postulated a thick layer of basaltic rocks of probable Miocene age, directly north of the Succor Creek area, possibly a remnant of a more extensive sequence, preserved by subsidence of the western end of Snake River Plain, probably with basaltic accumulation concurrent with subsidence. The outpouring of the basalt probably accompanied rifting of the upper crust under the Plain, which resulted from NE lateral spreading. If this is correct, the western Snake River Plain was a rift in Miocene time. In the northern part of the Succor Creek area, this subsidence may have been accompanied by penecontemporaneous accumulation of silicic ash deposits and weathered residuum by fluvial transport from the Idaho Batholith (Kittleman et al., 1965).

This tectonic boundary or suture is a zone of weakness through the crust, whether or not it was reactivated in mid-Miocene time. It could be the locus for the origin of a mantle plume from the asthenosphere or a propagating fracture system. Mantle plumes may be part of the non-arc related zones of continental rifting, or transform faults such as the Snake River Plain (Fig. 13). Morgan (1972) estimated the mantle plume, now located under Yellowstone National Park, to be about 150 km diameter, and to be rising at the rate of about 2 m/yr from deep in the asthenosphere into the lowest part of the mantle. More pertinent is Morgan's proposal that the Yellowstone mantle plume is structurally related to the northeast end of the Snake River depression. He considered that it arrived at this position after traversing southern Idaho along the course of the Snake River Plain. He and others (Suppe et al., 1975) considered the North American plate to have moved generally westward across a mantle plume that originated in the Owyhee area, at the position of the above mentioned suture, about 15 to 20 million years ago. The rate of eastward net migration of the mantle plume under the Snake River Plain was estimated at about 2.5 cm/yr by Armstrong et al. (1975).

Kirkham (1927, 1931) first postulated the Snake River Plain to be a downwarped plain, depressed to about 6,000 m below sea level. However, later studies clearly demonstrate the extensive, *en echelon,* NW-directed faulting, and any downwarp probably developed immediately prior to or concurrently with the deposition of the Sucker Creek Formation. This would account for the very rapid northward thickening of the Sucker Creek surface-type volcaniclastic sediments deposited in the western end of the depression.

Suppe et al. (1975) noted that the lowest stratigraphic unit in this region of Idaho is clearly associated with this propagating fracture or migrating hot-spot

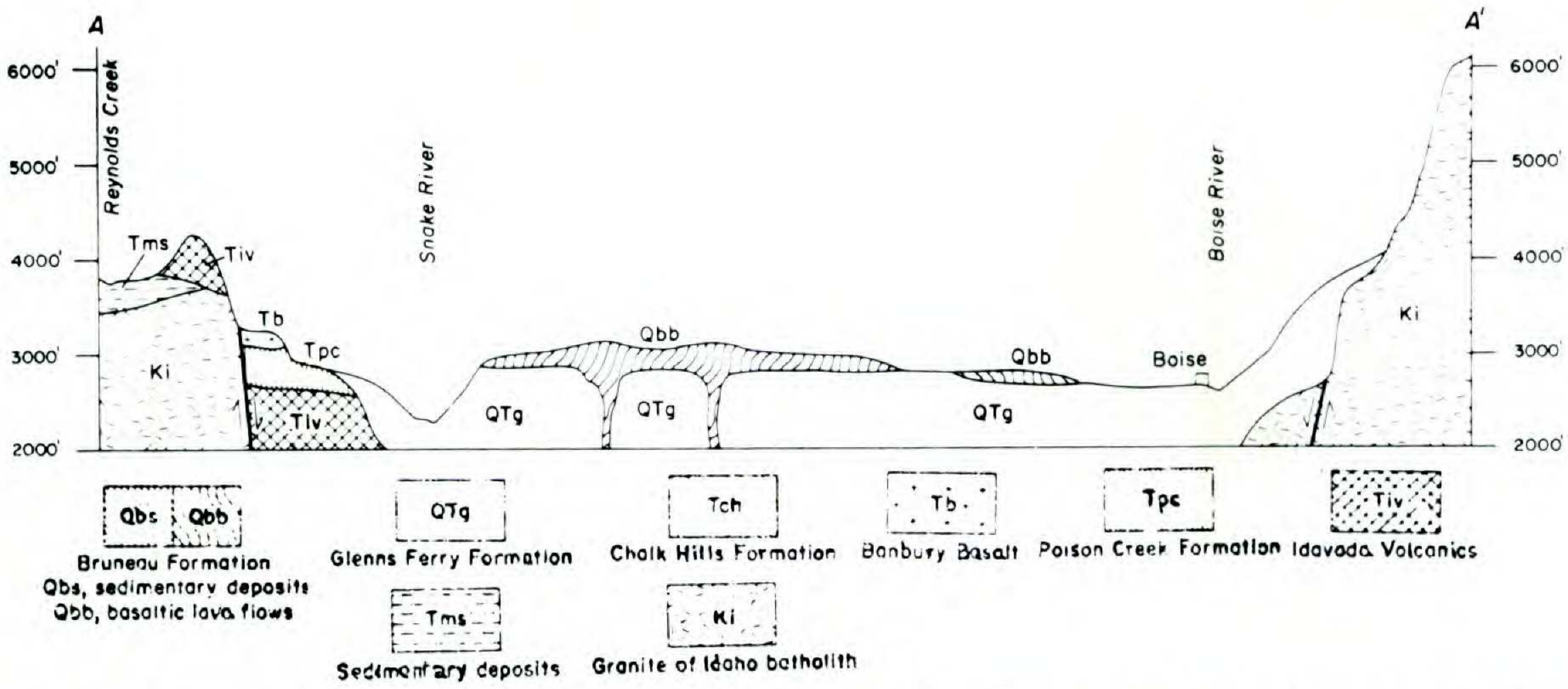

FIGURE 13. Diagrammatic geological cross-section from Reynolds Creek across the Snake River Plain through Boise, Idaho, showing the relationship of the graben structure of the Snake River Plain to the surrounding "horst" blocks. The Tms pattern at the far left represents the Sucker Creek Formation and possibly later sedimentary formations (Pliocene Poison Creek Formation). The Pliocene Idavada Volcanics (Tiv) overlie the Miocene sedimentary rocks unconformably. The basement rocks here are Cretaceous and earlier granites of the Idaho Batholith. Welded-ash flows of the Idavada Volcanics locally overlie the Sucker Creek Formation northwest of the Owyhee Mountains in a similar fashion as indicated on the cross-section just east of Reynolds Creek. (From Malde & Powers, 1962, Upper Cenozoic strata of the Snake River Plain, Idaho. Bull. Geol. Soc. Amer. 73: 1203, fig. 2.)

and is the earliest deposited portion of the time-transgressive Idavada Volcanics that overlie the Sucker Creek Formation in the western Idaho region. The age has been determined as early Pliocene on the basis of vertebrate fossils (Malde & Powers, 1962). These volcaniclastics are restricted to the uplands north and south of the Snake River and are cut by northwest trending faults that are probably related to the diastrophism that outlined the western Snake River Plain (see Fig. 3).

Suppe et al. (1975), following Morgan (1972), have reasoned that the Snake River Plain downwarp developed in the wake of the northeastward moving mantle plume at 2.3–2.7 cm/yr toward the Yellowstone area where it is today. They suggested the migrating domal uplift associated with the hot-spot is about 150–300 km in diameter, and the elevation of the updome above the region to the north and east of Yellowstone today is about 2 km maximum.

If this analogue is applied to the Oregon-Idaho border area at the time of the initiation of the dome, 15 to 20 m.y.b.p., the Owyhee and Succor Creek area may have had similar ephemeral elevation in mid-Miocene, which decayed in 3–4 m.y. to more nearly the present elevation, as the North American plate moved northwestward above the plume. If the domal uplift was initiated at the suture line of the Precambrian-Phanerozoic boundary in the vicinity of the Owyhees, there also may have been a westward or northwestward tilt of plateau-like proportions of this whole region, a paleoslope dipping off this ephemeral dome in a manner similar to that postulated for the Colorado Plateau by Suppe et al. (1975, p. 424).

A second basic explanation for the development of the Snake River Plain–Yellowstone system was proposed by Smith (1977) and Christiansen and McKee (1978). The essence of this concept, which also may result in conspicous elevation of the caldera, is that the system is a plate interaction phenomenon (Christiansen & McKee, 1978, p. 306). This interaction of the North American, Pacific and Farallon (Juan de Fuca remnant) plates began at least 29 m.y.b.p., but from about 17 m.y.b.p. the principal stress has been between the North American and Pacific plates. This resulted in two zones of lithospheric extension and stress relief at the northern margin of the Great Basin, a transform boundary; the Snake River plain to the east, and the Newberry system to the west, which is essentially coordinate with or parallel to the Brothers Fault zone (Fig. 3).

Iyer et al. (1981) have identified the presence of a large, low-velocity, magmatic body under the Yellowstone caldera, which may extend only to a depth of 200 to 300 km. The top of this partially molten body has been estimated at about 10 km. One possible model involves a region (or regions) of melting in the asthenosphere, upward migration of the magma, and secondary large-scale melting of the lower crust. Though this model and these interpretations would rule out the Morgan (1972) and later postulations of a deep mantle plume (hot-spot) or chemical plume (Anderson, 1975), and other explanations, it would support the proposals by Green (1971), Smith (1977), and Christiansen and McKee (1978), that the Snake River Plain–Yellowstone caldera are part of a propagation fracture system of the lithosphere, through a series of northeastward migrating calderas, with Yellowstone at present at the northeastward end of this fracture. This system is presumed to have followed a pre-existing zone of weakness (transform fault?) in the lithosphere.

This model does not require significant upwelling but does invoke thermal expansion under or near the zone of stress. But the development of calderas at successive stations along the route of propagation (here along the transform boundaries) is usually accompanied by ephemeral uplift and eventual collapse. Pelton and Smith (1979) in a review of possible causes of uplift associated with hot magmatic bodies underlying calderas, noted that the present Yellowstone caldera is 80–100 km maximum diameter, but other Snake River Plain caldera are estimated at 150 to 300 km. They also document the uplift of the Yellowstone caldera at the average rate of 14 mm/yr since 1923 (=1,400 m/100,000 yr). This time frame and magnitude of uplift greatly exceed that which would be required for distinctive shifts from bottomland/slope deciduous and evergreen dicot floras to montane conifer-dominated vegetation, postulated for the Succor Creek region in mid-Miocene.

Paleoelevation Variation of the Succor Creek Depositional Sites

We have postulated cool but highly equable climatic conditions for the Succor Creek region during the middle Miocene. Additional uplift in the Succor Creek area, relative to the present elevation of the region, would be required to obtain the cool thermal regime implied by the flora. Normal thermal lapse rates are of the order of 0.65°C/100 m (Miller & Thompson, 1975), and we suggest the character of the pollen flora indicates the Miocene elevation of the region must have been in the range of several hundred to 1,000 m higher than today.

Disparity between presumed paleoelevation of Miocene and Pliocene floras and present elevation of a region are not uncommon. A relatively low elevation

Miocene surface (i.e., below 600 m) was identified by Axelrod (1962) on the basis of fossil vegetation data for the Lake Tahoe area of California, which presently has an elevational range of 1,500 to 3,000 m.

Geological evidence provides several possible factors, some of which may be interrelated, that may have resulted in a distinct elevational differential between the Succor Creek region and surrounding areas. One factor may have been the development of a basin area to the north of the Succor Creek region due to the northwestward extension of the Snake River Plain rift or graben structure. There is ample evidence that sufficient downwarp or graben-type basin developed concurrently in the mid-Miocene to accommodate accumulation of 1,500 to 2,000 m of volcaniclastic rocks in the Sucker Creek Formation (Warner, 1977). The relative thinning of the formation southward in the Succor Creek area indicates a difference in elevation of several hundred meters. The Succor Creek area may have been subjected to significant uplift contemporaneous with the development of the flora. Brott et al. (1978, p. 1706) postulated that, beginning about 18 m.y.b.p., the Oregon-Idaho border area rhyolitic ash-flows must have been associated with ". . . a regional uplift of several hundred meters above the surrounding terrain, caldera formation at the source of the extrusives, and large-scale hydrothermal activity . . . ." This center of rhyolitic volcanism moved gradually eastward and, after 3–4 m.y., the area surrounding the original scene of eruption had subsided by 500 m or more.

Paleobotanical evidence for cool but equable climates appears sufficient to support this interpretation for the Succor Creek Flora. This is discordant with the somewhat warmer, but similarly equable, paleoclimates postulated for other contemporaneous floras in the region. However, sufficient structural evidence exists to provide a rational explanation of this anomaly. The elevation of an area need not remain constant, even over relatively short time spans, and such factors must be considered in analysis of Tertiary climates based on geographically and temporally distinct floras.

Volcanic Episodes as Related to the Succor Creek Flora

Mid-Miocene volcanism was an important event throughout Oregon and Washington, and, in theory, over a great part of the circum-Pacific area (McBirney et al., 1974, p. 587). The most intense volcanic episode in the Miocene is coincident with and directly related to the Columbia River Basalt outpourings, dated by Watkins and Baksi (1974) as beginning about 16.7 m.y.b.p. and lasting about 2.5 m.y. A corresponding and related center of activity to the Columbia River Basalt episode was located further west in the Western Cascade Mountains. There, a thick sequence of andesitic lava, the Sardine formation, comprises the main body of volcanic rocks in that region. These two great sequences of volcanic extrusives represent the most intense volcanism of the Pacific Northwest in Cenozoic time (McBirney et al., 1974, p. 586). The silicic lavas, ash-flows, and tuffs of the Succor Creek area and surrounding regions, south of the Columbia River Basalts (Fig. 3), represent episodic outbursts over much of this same time period. The source of these volcanics has been extensively occluded by accumulations during two much more recent extended episodes of volcanism, late Miocene–

Pliocene (9–11 m.y.b.p.) and late Pliocene–Quaternary (3.4–5.7 m.y.b.p.). The positions of some of the latter andesitic cones are indicated between the siliceous tuff fields on Figure 3.

Davis (1977, 1979) noted that, on the average, the Columbia River Basalt flows may have erupted every 10 to 20 thousand years with an average outpouring of 10 to 20 km^3. Some single flows were even larger, at least one reaching the Pacific ocean near the mouth of the Columbia River (Davis, 1977, p. 33; 1979, p. 43). The magnitude of this episodic destruction and the widespread distribution of even single flows, which repeatedly destroyed the vegetation over several thousand km^2, is difficult to comprehend. It is also possible that the siliceous tuffs, ash and rhyolites, which erupted south of the main expanse of the Columbia River Basalt field (Fig. 3), throughout the area of the Sucker Creek Formation, had a similar episodic time frame. We have estimated an 8,000 and 10,000 year period of accumulation of the 200 m thick Sucker Creek Type section and 100 m thick Whiskey Creek section, respectively. There may be more than coincidence in the similarity of episodic time intervals postulated, for the deposition of the plant-bearing ash and tuff beds, which have been derived from two different lines of evidence. Episodic volcanism is well-represented in the Succor Creek area. At least 16 successive lava flows of middle Miocene age make up the Owyhee Basalt near the Owyhee Reservoir, just west of the Type section (Watkins and Baksi, 1974). The earliest lava (no. 16) has Reverse paleomagnetic polarity; lavas no. 15 up through no. 3 have Normal polarity; the two uppermost are transitional. The time interval represented by the 16 flows and the intervening unconformities, is not more than 0.8 m.y. (13.9–13.1 m.y.b.p., Watkins & Baksi, 1974).

In both the Columbia River Basalts and the siliceous pyroclastic deposits of this area, it is probable that only small portions of the total area of distribution of the Sucker Creek Formation were buried by tephra from each eruption, but in successive eruptions alternate areas were covered. The extent of peripheral destruction of vegetation around the perimeter of each successive area buried under the pyroclastics was probably much more widespread than that from the recent Mt. St. Helens episode.

There is good evidence that geological factors, i.e., direct or side effects of tectonics and volcanism, may have contributed to the cooler episodes indicated by the presence of the Montane Conifer Paleoassociation in the Succor Creek Flora. It is possible that the cooling of the regional climate is directly attributable to sustained clusters of volcanic episodes that were the source of injection into the upper atmosphere of enormous quantities of very finely divided ash particles (discussed in the following section on Sedimentation). Robock (1979) demonstrated good correlation of the amount of volcanic dust in the atmosphere with average surface temperatures of the Northern Hemisphere during the past 400 years.

Flohn (1979) proposed that the intensified stratospheric dust layers resulting from volcanic eruptions may cause very rapid changes of temperature, with the intensity of cooling reaching the order of 5°C/50 yr, and a duration of centuries for such cool periods. The cooling results from both absorption and backscattering of part of the sun's radiation by the "dust veil" (Flohn, 1979, p. 140). He suggested that the frequency of such episodes may be on the order of one- to ten-thousand years. Though his study was directed toward explanation of sudden cooling in interglacial periods over the last 7×10^5 yr, he suggested that very rapid cooling and maintenance of cooler climate for such periods is not restricted to the Pleistocene. Such events may be related to periods when "clusters of volcanic eruptions" have occurred. Axelrod (1981) indicated it is unlikely that single volcanic events have had more than ephemeral climatic effects.

Bray (1979) discussed another factor influencing the lowering of temperatures as a result of volcanic activity, which is considered here in respect to its possible effect on vegetation destabilization. He suggested the increase in albedo, which would have characterized the regions covered by extensive, light-colored, ash deposits from eight particular eruptions during the Pleistocene, would have ranged from about 0.06% to 0.41%, depending on the reflectance quality of each different ash blanket. Such increases in albedo would have lowered the temperatures regionally from 0.07° to 0.41°C, with greatest cooling in and surrounding the ash-covered terrains. The extent of ash coverage for each volcanic event may vary considerably and the accompanying albedo-induced lower temperatures persisted for many decades (Bray, 1979). The rhyolitic ash layers of the mid-Miocene are believed to have been very widespread in eastern Oregon–western Idaho (see Fig. 3), and were very light-colored.

Regional increases in surface albedo, coupled with world-wide increases in atmospheric albedo can be assumed to be cumulative in their local effect. Where sufficient elevation was present, such as the ephemeral uplift of the region discussed previously, still further temperature depressions coincident with and following volcanic episodes might be expected. Regional snowfall may well have increased, leading to more extensive and persistent snowfields, which would have further increased regional surface albedo, intensifying the cooling produced by the surface ash layers. All of these phenomena are consistent with the expansion of the areal extent of the Montane Conifer Paleoassociation at different periods during Sucker Creek time.

Axelrod (1981) made extensive analyses of the historic effects of volcanism and its effect on terrestrial and marine life, particularly due to lowered temperatures as a result of episodes of extensive volcanic activity. He stressed the importance of the location of the volcanoes ("circulation tends to restrict dust veils resulting from Northern Hemisphere middle- and high-latitude eruptions to the regions north of lat 30°N, whereas dust from low-latitude eruptions . . . spreads over the entire globe . . . ," 1981, p. 1); the height of injection of the tephra into the atmosphere; and the size of the particulates of the ejecta. He noted that in addition to the cooling effect of decreased radiation reaching the earth's surface, the infrared energy radiated back from the surface is not contained by the atmospheric dust blanket.

Axelrod (1981) summarized the mid-Miocene changes in vegetation in the far Western Interior, including the Pacific Northwest, noting that thousands of km^3 of volcanic ash in the upper atmosphere lowered the mean temperature, which brought colder winters. This also strengthened the sub-tropical high-pressure cell, so that the frequency and amount of warm-season convectional precipitation also decreased. This would accelerate the disappearance of many of the warm-temperate to subtropical deciduous evergreens from the flora and result in a broad expansion of montane conifers at higher altitudes. We have noted the continued

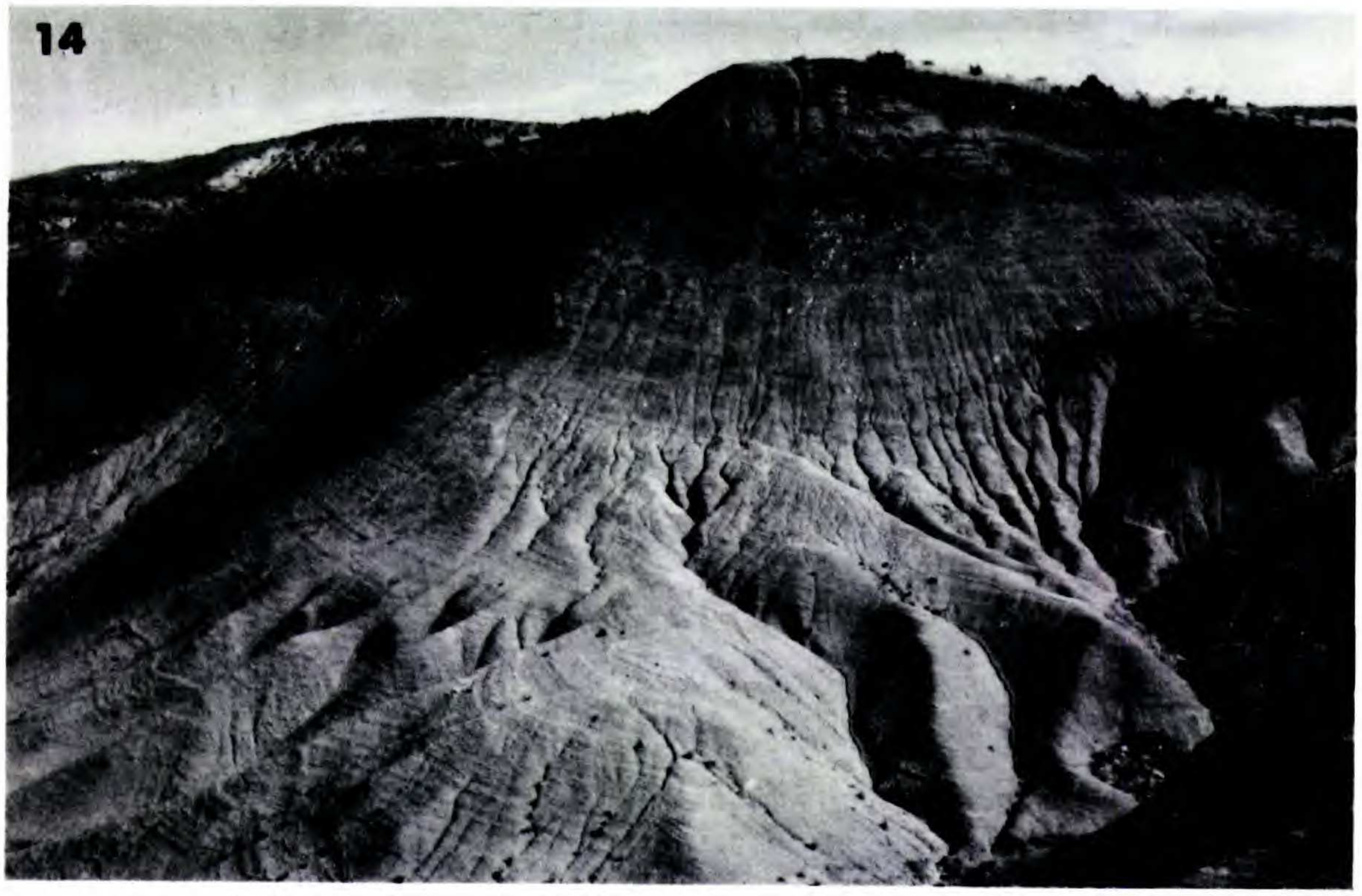

FIGURE 14. Lacustrine sediments in the Succor Creek area. Most lacustrine units in the study area are recognized on the basis of the generally thin-laminated, fine-grained sediments making up the strata, but outcrop exposures are typically too limited to indicate the geographic extent of the lake system. This shows a major outcrop of lacustrine sediments exposed in the Coal Mine Basin about 3 km east of the Whiskey Creek section (Fig. 1). The sedimentary laminations of this deposit are visible on the foreslope in the lower left of the picture. This unit consists of approximately 45 m of sediment and was sampled at intervals averaging approximately 50 cm. Some of the pits excavated to recover a continuous sequence of samples are visible on the slope face on the left side of the photograph. A total of 13 leaf-bearing horizons were documented within this unit.

presence of all these floristic elements in the region through Sucker Creek time, with repeated oscillation of the Montane Conifer Paleoassociation with the Bottomland/Slope community.

Sedimentation and Alteration of Sucker Creek Rocks

The source of the sediments that comprise the Sucker Creek Formation and the presence of fossils in some layers and their absence in others require some explanation. The Type section is adequate as a basis for discussion of most of the sections we have studied (Fig. 1). Kittleman et al. (1965) described in detail the lithologic, petrographic, and some mineralogic characteristics of about 25 of the definable beds in this section. We have restudied the exposures in the area, filled in some lithologic information of the concealed zones of Kittleman et al. from traceable beds in related exposures, and extended the base and the top of the section to include additional strata above and below. We simultaneously collected about 70 samples from the various layers for palynologic analysis. Some samples represent subdivisions of certain lithologic units defined by Kittleman et al., as indicated in Figure 10.

Most of the strata in this section are comprised of fluvially transported ash and pumice and some lacustrine deposits. A few beds were deposited directly

FIGURE 15. This shows a closer view of evenly-laminated, porcelaneous, lacustrine beds near the junction of Rte. 95 and Succor Creek road (Fig. 1), an early site for collection of Succor Creek plant macrofossils. Some of the layers within this sequence are indurated with chert, and typical Succor Creek leaf material occurs throughout. Pollen samples from this interval record a suite dominated by Bottomland/Slope and Montane Conifer elements, typical of the "climax" forest pollen signature throughout the area.

from air falls. Some of the layers are comprised of the finer size sediments, such as ash or pumice, flushed off the topographic highs and fluvially transported into the valleys and lower basins. Weathered materials from basaltic and rhyolitic flows and injections, and from extensive welded-ash beds from nearby areas, also contribute to some of the strata here.

A number of these beds contain fossil spores, pollen, fragments or burned shards of woody tissues of higher plants (fusain), and some algal cells and cysts including dispersed diatoms and massive layers of diatomite. A few beds contain larger fossils of fish, mammals and disarticulated vertebrates, and plant leaves, seeds, fruits, twigs, larger slabs of wood, and stumps. The larger plant remains usually occur in lignites, lignitic shales, lake beds (comprised of volcanic claystones (Figs. 14, 15), mudstones, siltstones, and diatomites), and occasional fluvial deposits. However, many of the lithologic units, comprising a significant portion of the thickness of the 200 m of exposed volcaniclastic rocks in the Type section, are barren of organic detritus. Pollen, spores, and woody detritus (fusain and vitrain) may have originally been present in many of these strata, which are now barren, though probably in very low percentages, volumetrically, due to a major dilution factor in beds of rapid ash accumulation. Entrapment of larger plant fragments may have taken place where the air-fall or water-laid ash accumulated over forest floor litter or where vegetation was killed and stripped by vented gases or hot or gaseous ashflows and was blown or washed into lake or fluvial basins.

Petrographic evaluation of various beds indicates a possible explanation for the absence of fossils from large portions of this 200 m section and other areas. The layers of pyroclastic sediments have been altered to variable extents. The ejected pyroclastics are comprised of fresh glass shards, formed from stretched and exploded glass bubbles, and angular pumice in a mixture of size fractions and mineral composition. Some of the beds in the Type section are largely comprised of such pumice (units K-20, K-29, and K-31, Figure 10, are predominantly unaltered glass shards in silvery-gray pumice). These contain no fossils. Many of the beds are extensively altered, mineralogically, often to 70% to 90% clay materials of several types. Bed K-14, for example, has 80% clay with some subhedral plagioclase, some coarse-grained, clear, angular quartz, and abundant authigenic zeolite minerals such as clinoptilolite, and some clasts of mafic or silicic scoria and rhyolite (Kittleman et al., 1965). Bed K-9 is very similar mineralogically, but slightly less altered and with definable relic glass texture. This layer contains no plant fossils but a considerable number of water-distributed, disarticulated (some waterworn) vertebrate bones. Bed K-11 is an altered pumiceous lapillistone which probably originated as an air fall.

The presence of zeolite minerals, devitrified pseudomorphs of glass, high clay content, and occasional plagioclase feldspar (andesine) such as in beds K-9, K-13 and K-14 (Kittleman et al., 1965), gives a strong indication of very rapid alteration of the minerals in some zones. Hay (1963, 1978) has assigned most natural zeolite mineral occurrences to one of six types of geologic environments or hydrologic systems, three of which may be represented in the Sucker Creek stratigraphic sequence: saline-alkaline lakes; saline-alkaline soils; and percolating water in an open hydrologic system (such as the John Day Formation strata, which are similar to and 120 km northwest of Succor Creek). The zeolites form rapidly during and after burial or accumulation and in saline-alkaline lake environments, through the action of dissolved sodium carbonate-bicarbonate in a pH of about 9.5. Vitric tuffs may alter to zeolite under such conditions in less than a thousand years (Hay, 1978, p. 137). Surdham and Sheppard (1978, p. 152) noted that along Pleistocene Lake Tecopa, California, fresh glass occurs along the margin and inlets of the ancient lake. Thus, these different phases of alteration may be virtually penecontemporaneous, geologically speaking. Mumpton (1978) noted that Sheppard and Gude (1968) have correlated zeolite mineralogy with similar patterns in a number of western states of the United States.

Such rapid and extensive alteration in any sediment will be detrimental to many types of fossil remains. Pollen and spores are particularly degraded in high pH environments. Some of the water-laid volcanic ash beds, constituting a significant part of the stratigraphic sections that we have studied, are so extensively altered that it is not surprising they are barren. The post-depositional geochemical environment is therefore incompatible with the preservation of pollen and spores in many of the fluvial and lacustrine volcaniclastic rocks in this region.

MODERN REGIONAL ANALOGUE OF SUCCOR CREEK COMMUNITIES

The proposed post-disturbance successional hypothesis requires spatial and temporal intermingling of broad-leaved, coniferous, and xeric community elements on a topographically variable landscape. Although the assumed paleoclimax communities are typically of higher floristic diversity than extant communities, the Succor Creek area does support communities that are analogous in aspect to some components of our Miocene vegetation reconstruction. The extant vegetation of the Succor Creek region, below 1,500–1,800 m is a sagebrush-grass-forb steppe. A juniper-sage savanna vegetation is present erratically above about 1,600 m elevation, depending on the degree of protection by slope exposure and the size of the area. Woodland-shrub riverine communities appear beginning at slightly lower elevations. The present regional sagebrush-grass-forb vegetation is quite unlike the diverse vegetation array characteristic of Miocene climax communities constituting the Succor Creek Flora but is probably similar in aspect to the early post-disturbance sere. Other analogues may be noted in the Silver City area of the Owyhee Mountains in Idaho, south of the Succor Creek silicic volcanics (Fig. 3). Elevation throughout most of the Succor Creek region is about 1,200 m, but granitic peaks in the Owyhee Range rise to over 2,400 m. The Snake River, 30–35 km north northeast of the 2,450 m War Eagle Peak near Silver City, Idaho, is at 685 m elevation, and the broader reaches of the lava-covered Snake River Plain here (see Fig. 13) are between 750 and 850 m. Therefore, in 25 km, the topographic relief above the Snake River Plain is over 1,600 m.

The western side of the range supports increasingly diverse woody vegetation above 1,500 m due to the generally lower temperature regime and reduced evapotranspiration in the uplands. Figure 17 shows one site, at an elevation of 1,625 m, that supports a variety of community types somewhat analagous in aspect to the vegetation postulated for the recovery periods following disturbance in Succor Creek time. Dry, south-facing slopes (Fig. 16) support the sagebrush-grass-forb steppe characteristic of the region, with *Juniperus* widely scattered on the slopes. The limited riparian zone along the course of Jordan Creek supports a surprisingly diverse broad-leaved element including *Salix* (several species), *Populus* (2 species), *Acer, Alnus, Mahonia, Prunus, Ribes, Rosa, Rubus,* and *Sambucus*. The overall aspect of this riparian assemblage may be similar to that of the post-disturbance vegetation of the Miocene, except for the much greater diversity of the Miocene assemblage. Somewhat more mesic north-facing slopes (Fig. 17) support forests of *Pseudotsuga,* with an admixture of *Picea* and *Abies* above 1,800 m. The present montane forest is undoubtedly similar in aspect to that of the Miocene although *Pseudotsuga* has not been recognized in the fossil flora to date, and *Pinus* is missing today from the Owyhee area. The absence of pine from the extant flora appears to be a result of having been eliminated by the raising of the dry-line below, a condition that probably developed during the hypsithermal period (Bowman, 1911, pp. 206–207; Daubenmire, 1978, p. 172). The effect of this high "dry-line" below and a static or low "cold-line" above was to "squeeze out" the pine. Pine apparently has been unable to recover across the xeric barrier of the sagebrush-grass-forb steppe.

Conclusions

Historically, the individual macrofossil florules from the Succor Creek area have generally been treated as a single entity, the Succor Creek Flora. Such a single grouping of the florules is justified, based on the limited geographic distribution of the florules and the relatively limited time span (1–2 m.y.) represented by episodic volcaniclastics and flows totalling between 600 and 1,800 m in thick-

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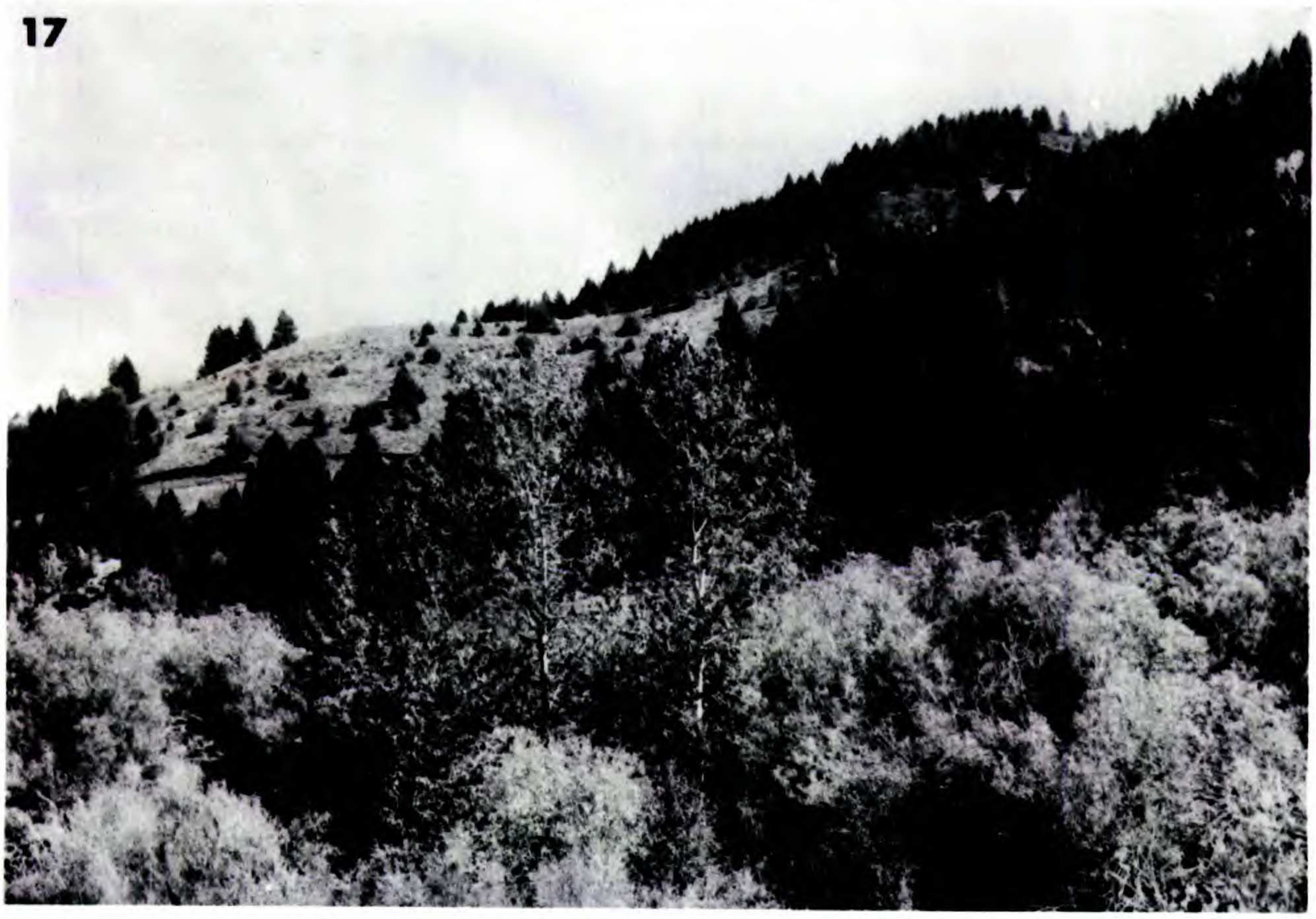
17



FIGURES 16–17. Modern vegetation in the Owyhee Mountains east of the Succor Creek area. Both of these photographs, taken along the course of Jordan Creek at approximately 1,700 m elevation, show a mosaic of community types with floristic composition remarkably like that of some of the Miocene communities, when allowances are made for the absence of "exotic" taxa in the extant communities. The drier south-facing slopes shown on the left of Figure 16 support a sagebrush-

ness. With due recognition of spatial, elevational, and temporal variation between florules, the collective flora does represent a meaningful data set. Treating the complex in this manner, however, obscures a great deal of additional data that is critical in any interpretation of the flora relative to paleoclimatic trends or the pattern of modernization of floras within the region. The record of paleoclimatic trends during the one to two million year span of Sucker Creek time is now represented by discontinuous series of deposits, each laid down in a few thousand to a few tens of thousands of years.

Episodic volcanic disturbance and, to a lesser extent, other disturbance factors such as fire and localized flooding, resulted in periodic destabilization of forest habitats, with the consequent widespread occurrence of distinctive successional communities. Volcanic ash input, by air-fall or fluvial transport to local sedimentary basins and lakes, preserved plant macrofossils that represent some of the component species of localized communities that were part of the "climax" mosaic, as well as communities of a successional nature. Much of the recorded diversity of Succor Creek macrofossil florules can be attributed to disparate sampling of community types, together with disproportionate distribution and preservation of plant parts.

Unfortunately, the Succor Creek Flora, and most of the classic middle and late Tertiary floras of the Pacific Northwest, have lacked the close stratigraphic and palynological control required to recognize the presence of such community disruptions and the consequent successional vegetation dynamics. The fact that the floras in the region are preserved in fluvial volcanic ash deposits and volcaniclastic lake sediments, sometimes interbedded with diatomaceous beds strongly suggests that such disruptions and processes can be expected to have been widespread in occurrence. Many floras do represent samples of climax communities. However, if significant variation in diversity and composition exists between various florules of a flora, due consideration should be given to the possibility of the existence of distinctive communities representing seral stages. Only when climax associations can be identified with reasonable certainty, can meaningful regional paleoclimatic reconstructions be made. Postulating climatic trends based on stratigraphically disjunct and/or geographically distant floras of unknown relationships, as has been the practice, results in extensive obfuscation of the true nature of both short and long-term shifts in plant communities. Our studies indicate that in the short-term, centuries to tens of thousands of years (or even on a scale one order of magnitude greater), small-scale oscillations in temperature parameters characterized the climate of the Pacific Northwest during this part of the Miocene. Although the causes of such small-scale temperature oscillations are conjectural, it is reasonable to assume that temperatures in the region were controlled by some of the same factors operating today; i.e., elevation, relief, continentality,

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forb community with scattered *Juniperus*. The stream valley, lower right of Figure 16 and foreground of Figure 17 supports a reasonably diverse array of broad-leaved woody taxa including *Salix*, *Populus*, *Alnus*, and *Ribes*. North-facing slopes (upper right of Fig. 16 and Fig. 17) support stands of *Pseudotsuga* with scattered *Picea* above 1,800 m.

shifts in albedo caused by extensive new ash deposits, reduced insolation following volcanic eruptions, and earth orbit mechanics.

In areas of great topographic relief, such small-scale thermal changes would have a minimum effect on total vegetation components of a region. Where slope gradients are high, modest changes in the elevation of ecotones need not result in significant changes in the areal extent of specific communities and most communities could continue to find suitable niches in the variety of microenvironments in the valleys and protected slopes of a mountainous terrain for their general continuance. In contrast, where broad, sloping plateaus, or perhaps highland areas with very low relief, which we have postulated here, or in other places where areally extensive low-slope gradients characterize a region, even small regional temperature changes can cause pronounced areal shifts in community distribution. This would be particularly true for the various communities making up the regional vegetation mosaic, many of the components of which were under thermal stress near the margins of critical thermal fields.

The Succor Creek flora was, like any extant flora, a diverse mosaic of community types in dynamic equilibrium with climate. However, the vegetation was subjected to episodic and probably massive physical disturbance, which served to mold the dynamics and composition of the flora independent of cliseral shifts in community distribution. This situation was undoubtedly not confined to the Succor Creek area but was probably a regional phenomenon. Consideration of this dynamic response to disturbance, in concert with factors such as geographic, elevational, and temporal differences between Tertiary floras in the Pacific Northwest, may materially assist in the problem of modeling Tertiary climatic trends and vegetation modernization within the region.

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